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BRITISH MUSEUM
20 JUL 1961

A CONTRIBUTION TO THE ODONTOLOGY OF *OREOPITHECUS*

BRITISH MUSEUM
NATURAL HISTORY

P. M. BUTLER
AND
J. R. E. MILLS

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
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A CONTRIBUTION TO THE ODONTOLOGY OF *OREOPITHECUS*

BY

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BRITISH MUSEUM NATURAL HISTORY

A CONTRIBUTION TO THE ODONTOLOGY OF *OREOPITHECUS*

By P. M. BUTLER AND J. R. E. MILLS

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SYNOPSIS

The upper teeth of the British Museum specimen of *Oreopithecus bambolii* are described. These include the hitherto unknown Pd^4. The wear facets on the milk-molars and molars are interpreted in terms of occlusal relations. Comparisons are made with Cercopithecidae, with fossil and Recent Pongidae and with Hominidae. It is concluded that *Oreopithecus* cannot be placed in any of these families, but is an independent derivative of a primitive catarrhine stock. Its molariform teeth show most resemblance to those of the primitive Pongidae, for example *Proconsul*, but they do not support the theory of hominid relationships. Characters shared with Hominidae, such as the shortened face and reduced canines, are probably the result of parallel evolution.

I. INTRODUCTION

Though known since 1872, *Oreopithecus bambolii* Gervais, from the Pontian of Italy, has still not been fitted satisfactorily into the classification of Primates. It has been restudied in recent years by Hürzeler (1949, 1958), who has argued in favour of hominoid, rather than cercopithecoid, affinities, and has pointed out a number of resemblances to man which he believes to be significant. The British Museum possesses a specimen of *Oreopithecus*, hitherto overlooked, in which the upper dentition is very well displayed. In view of the interest aroused by Hürzeler's work, the authors decided to make a detailed study of this specimen. As a result they have reached conclusions which diverge from those of Hürzeler, particularly in regard to the relationship between *Oreopithecus* and man.

II. THE BRITISH MUSEUM SPECIMEN

1. *Condition and identity.* The provenance of the specimen (Brit. Mus. Palaeont. Dept. M 11555) is not recorded, but the matrix is lignite, like that of other known specimens of *Oreopithecus*, and an Italian origin is reasonably certain.

The specimen consists of a palate, rather severely distorted by lateral crushing (Pl. 1). On the left side are the unerupted permanent canine, the two milk-molars, the first two molars and an unerupted third molar ; P^3 is partly visible above Pd^3. The crown of the canine is intact ; Pd^3 lacks the buccal side of the crown ; Pd^4 is complete, though moderately worn ; M^1 and M^2 are only slightly worn, but the buccal half of M^1 and the anterobuccal part of M^2 have been broken away ; of M^3 only the anterior part of the crown is preserved. On the right side the milk-molars have been removed, and the crowns of the permanent canine and P^4 are fully preserved, but that of P^3 has been broken off ; M^1 and M^2 are severely damaged, but the unerupted M^3 is fully preserved. Owing to crushing, practically no characters of the skull can be made out : the left teeth have been pushed over medially, but the right teeth still retain their original relations to the palate.

Apart from some minor differences in the arrangement of ridges, the molars closely resemble the unworn teeth of *Oreopithecus bambolii* in the Basel Museum (Hürzeler, 1949, fig. 11). Comparison with a cast of the Florence specimen, I.G.F. 4332 (Hürzeler, 1949, fig. 10) reveals differences in the measurements of the teeth (Table I), and the presence of a small metacone on P^4, absent in the Florence specimen. These differences are probably insufficient to demand a specific distinction, and the British Museum specimen is therefore referred to *Oreopithecus bambolii*.

2. *Upper molars and milk-molars.* M^3 is longer than wide, and narrower posteriorly than anteriorly. Of the four main cusps, the metacone and hypocone are less high than the paracone and protocone respectively. The apex of the paracone forms an angle of about 70° when seen in buccal view, and the metacone is equally acute.

TABLE I

(Measurements of teeth in millimetres)

Oreopithecus		M^3	M^2	M^1	Pd^4	Pd^3 (as preserved)	P^4	P^3	C
M. 11555	Length (between contact points)	9·4	9·0	8·2	6·6	5·5	6·5	—	7·5
	Width (across anterior half of crown)	8·7	8·7	—	6·6	—	8·0	—	6·1
I.G.F. 4332	Length	9·8	9·3	8·2	—	—	5·6	5·8	6·7
(measured on cast)	Width	9·4	8·9	7·7	—	—	9·0	8·5	6·4

The complexity of the pattern is greatly increased by the development of well-defined ridges on the slopes of the main cusps, as well as by the formation of secondary cusps and cingula, clearly indicated in Text-fig. 1. These minor features show much variability in anthropoids (Remane, 1921), and it is not surprising that Hürzeler's specimens frequently differ in details from the British Museum specimen. For example, in one of Hürzeler's specimens there is no posterobuccal cingulum, and in another the posterobuccal crest of the paracone ends at the valley between the paracone and metacone (Hürzeler, 1949, fig. 11). Again, in the specimens figured by Hürzeler the posterior crest of the paracone turns towards the buccal side of the crown to meet the cingulum.

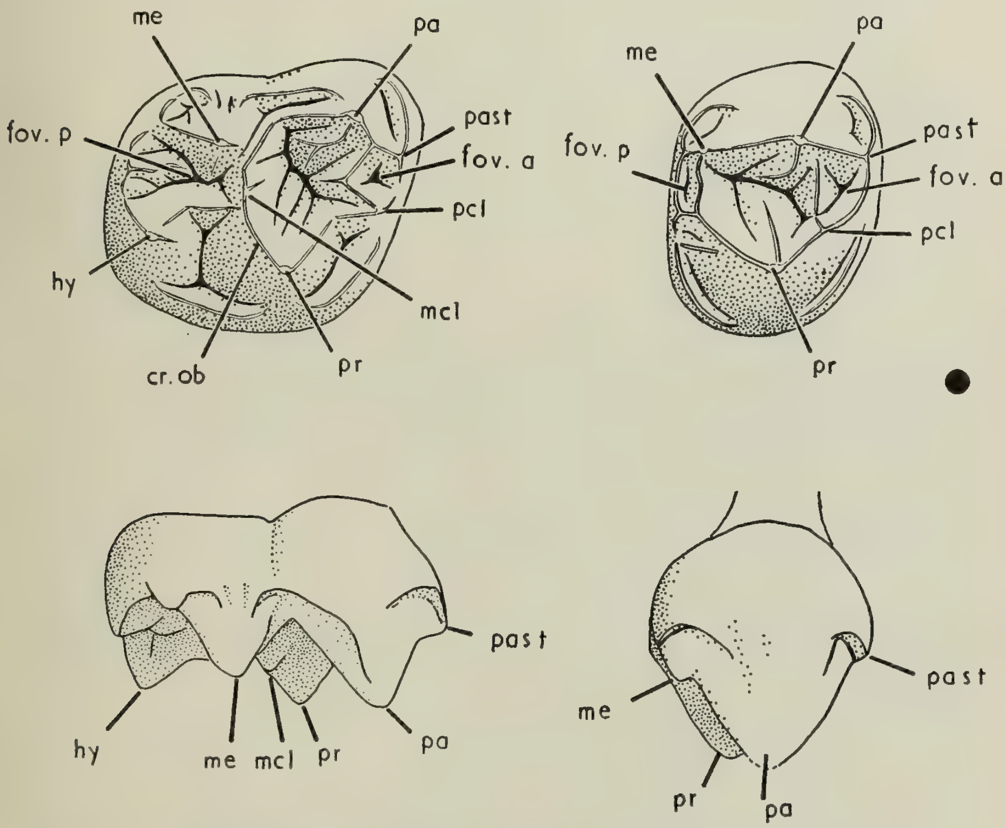

Fig. 1. *Oreopithecus bambolii* (Brit. Mus. M 11555). Crown and buccal views of right M^3 and P^4, × 5. *cr. ob*, crista obliqua; *hy*, hypocone; *fov. a*, fovea anterior; *fov. p*, fovea posterior; *mcl*, metaconule; *me*, metacone; *pa*, paracone; *past*, parastyle; *pcl*, protoconule; *pr*, protocone. In this and other figures ● indicates the anterior end.

There is a progressive change in the proportions of the crown as the pattern is traced forward through the molars and milk-molars (Table II; Text-fig. 2). The metacone of M^2 reaches a height of 2·9 mm. above the level of the buccal cingulum, compared with 2·1 mm. on M³. The hypocone of M² is also higher than that of M³, reaching the same height as the protocone. The posterior crest of the paracone, which on M³ unites with the buccal end of the crista obliqua, terminates on M² in a small cusp applied to the anterior side of the metacone, while the crista obliqua continues to the tip of the metacone. The fovea posterior of M² is divided by a crest which connects the metacone to the hypocone.

TABLE II

(Measurements in millimetres)

Oreopithecus (M. 11555)	M³	M²	M¹	Pd⁴	Pd³
Length (*a*)	9·4	9·0	8·2	6·6	5·5
Anterior width (*b*) (across paracone)	8·7	8·7	—	6·6	—
Posterior width (*c*) (across metacone)	6·8	7·8	7·8	6·5	—
Length of hypocone (*d*)	3·3	3·8	3·4	2·5	1·5
Ratios : *b*/*a*	0·93	0·97	—	1·00	—
c/*a*	0·72	0·87	0·95	0·99	—
d/*a*	0·35	0·42	0·41	0·38	0·27

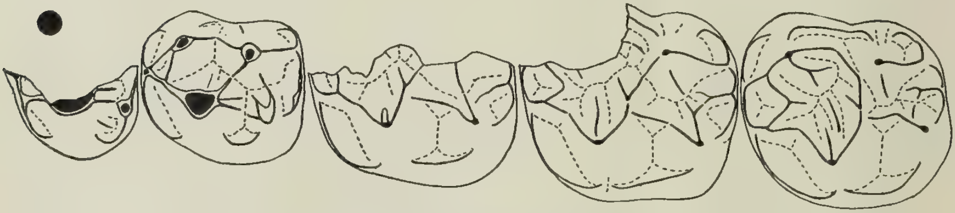

FIG. 2. *Oreopithecus bambolii* (Brit. Mus. M 11555). Left Pd³–M³, crown view. (M³ drawn in reverse from right side). × 3.

The buccal part of M¹ is missing, but the lingual part of the tooth shows little difference from M². The metaconule has become merged into the crista obliqua, and the region between the paracone and protocone is reduced in relative area and simplified.

Pd⁴ has most of the elements of the molar pattern, but shows a number of distinctive features. The height of the neck of the tooth, from the cingulum to the basal margin of the enamel, is only about 2·2 mm., whereas on the molars it is about 2·7 mm. The buccal cingulum is hardly distinguishable. The posterior crest of the paracone runs to the tip of the metacone. The crista obliqua also runs to the tip of the metacone, and there is no distinct metaconule. The fovea anterior is represented by a triangular area between the anterior crest of the paracone and an anterolingual crest which diverges from it at a small angle. Comparison with M¹ and M² shows that the protoconule is represented by the point of junction between the anterolingual crest of the paracone and the anterior crest of the protocone. On M³ and M² the posterior border of the fovea anterior is formed by a small cusp ; on M¹ this cusp merges with the protoconule, and on Pd⁴ it is absent. The fovea posterior of Pd⁴ is divided by a crest connecting the metacone to the hypocone, as on M¹ and M², but the cusp which in the molars develops on the posterior margin of the fovea is absent in Pd⁴. The hypocone is well developed, but slightly reduced in mesiodistal diameter relatively to the protocone. As on the molars, it is connected by a crest to the crista obliqua, but in addition there is a more lingual crest, which joins the hypocone and protocone directly.

Only the lingual part of Pd³ is preserved. It does not differ significantly from the tooth described by Hürzeler (1958, fig. 14). The protocone occupies most of the lingual part of the crown, the hypocone being reduced to a small cingulum cusp. The anterolingual cingulum is narrower than on Pd⁴. At its buccal end is the parastyle, worn away to a small exposure of dentine. The protoconule appears to have merged into the crest that connects the parastyle to the protocone. A crest joins the protocone and hypocone, as on Pd⁴ ; running parallel to this crest, but more buccally, is the crest which connects the hypocone to the crista obliqua ; more lingually there is a third crest, which passes down the posterior side of the protocone into the small cingulum basin between the protocone and the hypocone. Hürzeler's specimen shows that the metacone has merged into the posterior crest of the paracone, where it is represented by the point of junction of this crest with the crista obliqua.

3. *Permanent premolars and canine.* P⁴ is transversely oval in outline, but less transverse than in I.G.F. 4332. It is about as long as Pd⁴, but one-fifth wider. There appears to be only one buccal root. The high, acute paracone and protocone occupy almost the entire crown ; the posterior part of the molar pattern is developed on the premolar to only a rudimentary extent (Text-fig. 1). There is a diminutive metacone (absent in I.G.F. 4332), connected to the protocone by a crest which represents the crista obliqua. The fovea posterior is very small, and there is no hypocone. The fovea anterior however is a relatively large triangular area, bounded by the anterior crest of the paracone and an anterolingual crest that buttresses it. The protoconule is represented by a rather indistinct elevation on the anterior marginal crest. Buccal and lingual cingula are present, broken opposite the paracone and protocone respectively, as on the molars. A short crest passes down the posterior side of the protocone into the posterior part of the lingual cingulum, corresponding to a crest found on Pd³. The central fovea is a deep basin, the floor of which sinks towards the posterior end ; crests from the paracone and protocone pass down its sides.

The posterior part of left P³ is hidden by Pd³, but the anterior half of the crown is exposed and undamaged. It differs hardly at all from the corresponding part of P⁴.

The right canine is completely exposed, but the extreme tip of the cusp has been broken off. The left canine is intact, but it is visible only from the buccal and anterior sides. The base is longer than wide, as in the male canine figured by Hürzeler (1958, fig. 5), but in the proportion of height to length it resembles the female canine figured by Hürzeler (1958, fig. 6), which, however, is somewhat smaller.

No buccal cingulum is present, but there is a rather strongly developed lingual cingulum, as in the female canine described by Hürzeler. The fovea anterior is represented by a triangular groove between the anterior crest and an anterolingual crest. The more basal part of the anterior crest is accompanied on its lingual side by a groove which appears to correspond to the much more conspicuous anterior groove of the male canine. The protocone of the premolar is represented on the canine by a slight elevation of the cingulum. More posteriorly, the cingulum widens to form a basin, corresponding to the deepest part of the central fovea of the premolar. At the posterior end, a fragment of cingulum is cut off to form the equivalent of the fovea posterior. Thus it is possible to homologise the pattern of the canine with that of the premolar (Text-fig. 3).

The premolars and canine must have erupted after M². Their roots are already partly formed: the buccal root of P⁴ and the root of the canine have both attained a height of about 4 mm., although the canine is placed more deeply in the jaw than the premolars. A broken section through left M³ shows that the roots, and even the basal surface of the crown, had not developed, and therefore it seems that the milk teeth would be replaced before M³ had erupted.

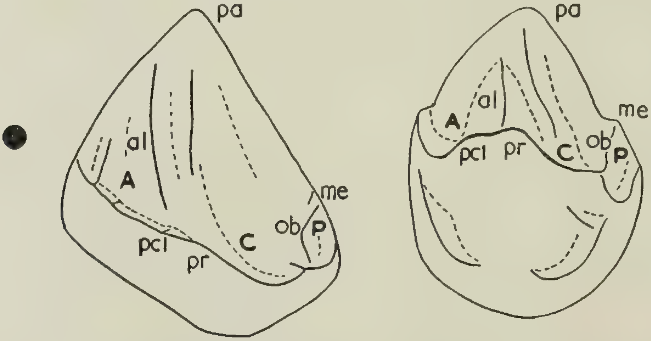

FIG. 3. *Oreopithecus bambolii* (Brit. Mus. M 11555, reversed). Left canine and P⁴, seen in lingual and slightly occlusal view. *A*, *C*, *P*, anterior, central and posterior foveae; *al*, anterolingual crest of paracone; *me*, metacone; *ob*, oblique crest; *pa*, paracone; *pcl*, protoconule; *pr*, protocone.

4. *Thickness of enamel.* Broken teeth show that many minor details of the pattern are represented in the dentine, the enamel forming a comparatively even layer over the crown. Using a micrometer eyepiece, measurements were made of the thickness of enamel, perpendicular to the dentine surface. On M³ it ranged from 0·4 to 0·8 mm., on M² from 0·5 to 0·8 mm., and on M¹ from 0·5 to 0·7 mm. On the milk-molars the enamel is thinner, the greatest thickness found being 0·4 mm. On the premolars and canine it is about as thick as on the molars.

5. *Wear facets.* Examination of the wear facets on the milk-molars and molars by reflected light under suitable magnification shows that each facet is covered by numerous fine parallel marks. These are readily distinguished from the smaller number of scratches, usually coarser and going in various directions, due to subsequent damage to the surface; the regular scratches must have been produced by chewing movements (Butler, 1952; Mills, 1955). The positions of the facets are shown in Text-fig. 4*A*, where they are shaded in accordance with the direction of the scratches. It will be seen that on some facets the scratches are transverse to

the tooth row, and on others they are oblique (posterobuccal-anterolingual). Transverse scratches were produced during rotation of the mandible about the ipsilateral condyle, the lower teeth being to the buccal side of the centric position; oblique scratches were produced during rotation about the contralateral condyle, when the lower teeth were to the lingual side of the centric position (see Text-fig. 4B).

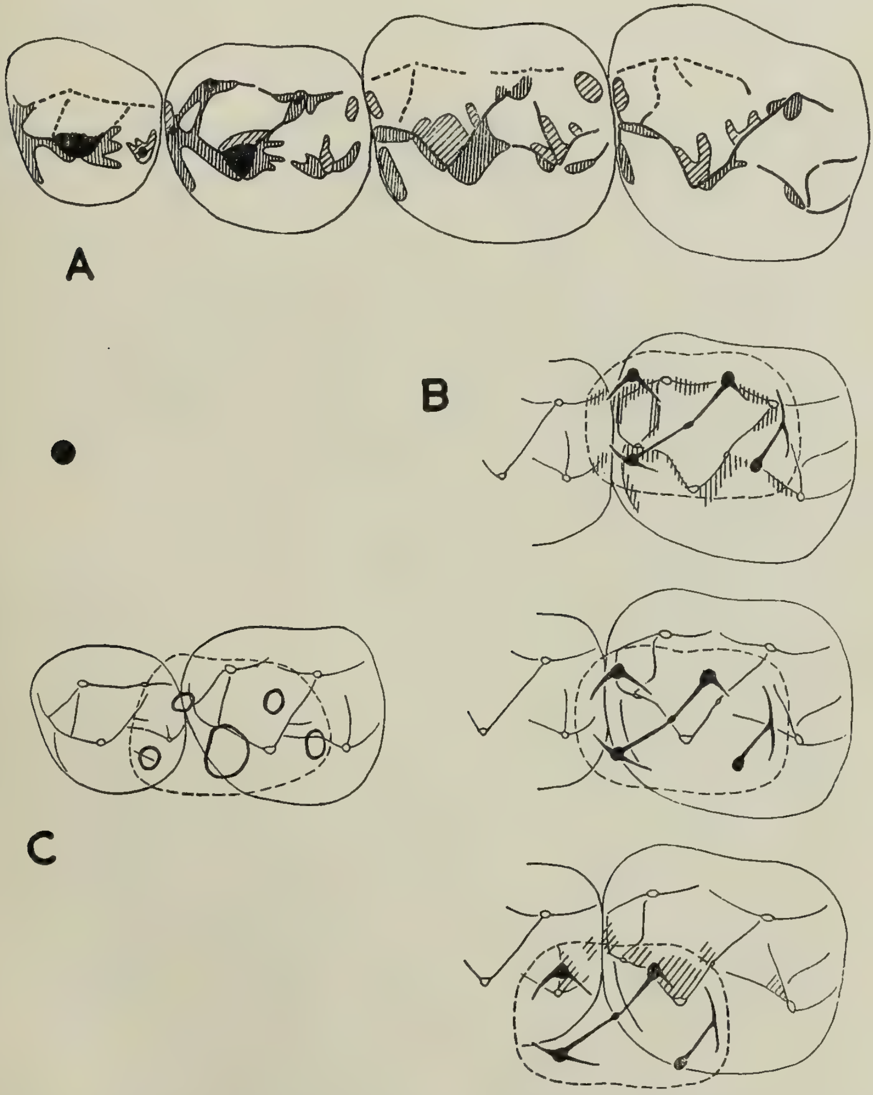

FIG. 4. *Oreopithecus bambolii* (Brit. Mus. M 11555). A, Wear facets on Pd^3–M^2, shaded according to the direction of scratches. B, Superposition of drawings of upper and lower molars, with lower molar in extreme buccal position, in centric position and in lingual position, to illustrate the formation of the wear facets. C, Superposition of Pd$_4$ (after Hürzeler, 1951) on Pd$^{3-4}$.

The scratches produced during transverse movement are not horizontal, but are inclined upwards towards the lingual side at a small angle (perhaps 20° : exact measurement is impossible as the orientation of the teeth is unknown). On M^2 the oblique scratches make an angle of 40° with the transverse scratches when seen in crown view ; the change in direction in the vertical plane is 35°.

In the absence of the lower teeth of the same individual, the analysis which follows is based upon the structure of the lower molars in the type mandible, which is well figured by Hürzeler (1949, fig. 2), and of which the British Museum possesses a cast.

During transverse movement the lower buccal cusps (protoconid, hypoconid) passed between the upper buccal cusps (paracone, metacone), and the lower lingual cusps (metaconid, entoconid) between the upper lingual cusps (protocone, hypocone). In its most buccal position the metaconid was in contact with the lingual face of the protoconule, and as it moved lingually it wore a facet on the anterolingual cingulum, as well as on the adjacent vertical faces of the protocone and hypocone. At the same time the entoconid, passing behind the protocone, wore a notch in the crest that joins the hypocone with the crista obliqua. The crest on the lower molar which connects the metaconid with the mesoconid apparently glided across the protocone-protoconule crest of the upper molar, forming a narrow facet at its edge. A facet on the lingual face of the metacone on M^1 and M^2 appears to be due to contact with the buccal face of the small hypoconulid ; a similar facet, produced by metacone-hypoconulid contact, occurs in the gorilla (Text-fig. 8). It is probable that the cuspule on the lingual side of the paracone, on the posterior edge of the fovea anterior, made contact with the mesoconid.

In the centric position the tip of the protoconid was situated immediately to the buccal side of the protoconule, and the tip of the hypoconid was in the middle of the trigon basin. As the lower molar moved obliquely forward and lingually from the centric position, parallel to the crista obliqua, the lingual surface of the hypoconid sheared against the buccal surface of the metaconule and the protocone, and the tip of the hypoconid passed through the notch between the protocone and the protoconule. At the same time the tip of the protoconid crossed the anterior cingulum and the fovea posterior of the tooth in front, to contact the buccal slope of the hypocone. In addition to the facet on the hypocone caused in this way, there is a small facet which faces more anteriorly, apparently due to contact with the hypoconulid ; it corresponds to a much larger facet present in the gorilla.

The interpretation of the occlusal relations of Pd^4 and Pd^3 is difficult because only one worn specimen of Pd_4 has been found (Hürzeler 1951), and Pd_3 is unknown. The metaconid of Pd_4 occupies a large area of the tooth and extends more posteriorly than in the molars, so that there is no distinct mesoconid, at least in the worn specimen. This large metaconid would be responsible for wear of the anterior cingulum of Pd^4 as well as that of the anterolingual side of the protocone and its anterior crest. The hypoconulid of Pd_4 is reduced, and its function of occluding with the metacone of Pd^4 has probably been taken over by the paraconid of M_1. In other respects the occlusal relations of Pd^4 probably resemble those of the molars. The large paraconid of Pd_4 must have extended forward for some distance across

Pd^3; and during transverse movement it would have passed behind the protocone of that tooth, wearing the facet on its posterior slope (Text-fig. 4B) ; it would thus replace the entoconid of Pd_3 which was presumably absent. The facet which covers the tip of the hypocone of Pd^3 was presumably formed by the protoconid of Pd_4 during oblique movement.

Pd_3 must have been a comparatively simple tooth, possessing a metaconid or its equivalent in the form of a posterolingual crest from the protoconid. It would be responsible for wear of the anterior side of the protocone of Pd^3 during transverse movements.

III. COMPARISONS

1. *Sources of material.* For comparative purposes, a study was made of specimens or casts of the upper teeth of all genera of living catarrhines and most genera of fossil forms. Extensive use was made of the collections in the British Museum (Natural History), and the authors wish to acknowledge the kind assistance given by Dr. E. I. White, F.R.S., Dr. T. C. S. Morrison-Scott, Dr. K. P. Oakley and their staff. Professor Sir Wilfrid Le Gros Clark, F.R.S. very kindly permitted them to examine specimens of *Proconsul* under his care. Thanks are also due to Dr. A. V. Stack and Dr. D. H. Goose for collections of human milk-molars.

2. *Comparison with Cercopithecidae.* The upper molar pattern of *Oreopithecus* shows little resemblance to the pattern found, with only minor variations, in all Recent Cercopithecidae and also in *Mesopithecus*. The differences may be summarised as follows :

Oreopithecus	Cercopithecidae
Protocone somewhat posterior to paracone.	Protocone directly opposite paracone.
Crista obliqua strongly developed.	Crista obliqua absent.
Protoconule and metaconule distinct.	Conules indistinct or absent.
Cingulum well developed.	Cingulum slight or absent.
Distinct fovea anterior.	No fovea anterior, unless it is represented by the basin cut off by the paracone-protocone crest.
During oblique movement of the lower jaw, the tip of the hypoconid passes through the notch between the protocone and the protoconule, the hypoconid shearing against the buccal surface of the protocone.	The tip of the hypoconid does not pass anterior to the tip of the protocone, but the plane of shear between the two cusps is rotated so as to face partly backwards in the upper molar (Mills, 1955).

Hürzeler (1949) is not convinced that the posterolingual cusp of the cercopithecid upper molar is a true hypocone, as it is not connected with the cingulum. If it is not a hypocone, the Cercopithecidae would be far removed from the Hominoidea, which possess a true hypocone : the common origin of the two groups would have to be sought at a tritubercular stage. It would also follow that *Oreopithecus*, in which the hypocone is connected with the cingulum, is on the hominoid branch. However, an enlargement of the cusp in Cercopithecidae, in combination with a loss of the lingual cingulum, could have so altered the relations of the hypocone that its origin from the cingulum is no longer apparent. As Remane (1951) has indicated, the less molarised forms of Pd^3 show that a derivation of the cercopithecid pattern from one more like that of hominoids is at least possible. Pd^3 frequently possesses a backwardly displaced protocone and a crista obliqua, and so shows some similarity to the molars of *Oreopithecus* (Text-fig. 10). If it is assumed that these features were formerly present in the cercopithecid molar, a distant relationship between *Oreopithecus* and the Cercopithecidae becomes feasible. In that case *Oreopithecus* would have retained on the whole a more primitive molar pattern than the Cercopithecidae (von Koenigswald, 1955).

Oreopithecus resembles most Cercopithecidae in that M^1 and M^2, instead of being transversely broadened teeth as in the majority of Eocene Primates, have become lengthened mesiodistally, so that the length equals or exceeds the breadth. In some living forms (*Trachypithecus*, *Presbytis*, *Presbytiscus*) the molars are still broader than long. Associated with the tendency to lengthen the molars is one, less advanced in *Oreopithecus* than in Cercopithecidae, for the posterior half of the molar to imitate the anterior half. In view of the differences of pattern it is very doubtful whether these resemblances imply relationship: they might be regarded as parallel adaptations to a herbivorous diet, found also in the Indriidae, for example. The height and sharpness of the molar cusps of *Oreopithecus* can be equalled in some Cercopithecidae, such as *Mesopithecus* and *Nasalis*. This is probably a primitive character inherited from a tarsioid ancestry.

Pd^3 of Cercopithecidae (Text-fig. 10) is much longer than wide; it possesses a distinct metacone, and in most cases is almost fully molariform. This type of Pd^3 is clearly specialised: in the great majority of Primates Pd^3 is premolariform, with at most a rudimentary metacone. *Oreopithecus* is much nearer to the primitive condition.

The canine is comparatively small in females of Cercopithecidae, especially in some short-faced Semnopithecinae, in which its general shape is very much like that of *Oreopithecus*. A precanine diastema in the upper jaw is often absent in female Cercopithecidae (e.g. *Rhinopithecus roxellanae*, *Presbytiscus avunculus* and *Nasalis larvatus*). The male canine is distinguished from that of the female by its greater relative height and the incomplete development of its lingual cingulum, as in *Oreopithecus*. It is, however, larger and more projecting than in *Oreopithecus*, and is further distinguished in that the groove on its anterior slope is continued on to the root (Hürzeler 1958).

3. *Comparison with Pongidae.* The upper molar pattern of *Oreopithecus* is close to the pongid type. The resemblance extends to the wear facets, showing that the occlusal relations were essentially similar (Text-fig. 8). In a number of respects, however, *Oreopithecus* differs from all known Pongidae:

(1) The cusps are more acute even than in the gorilla and gibbon. This character, which is shared with a number of tarsioids and cercopithecoids, is probably primitive (Text-fig. 7).

(2) The protocone is markedly V-shaped in crown view, its tip placed near the lingual border of the crown and far removed from the protoconule, from which it is separated by a deep notch. This feature is common in early Primates and is presumably primitive (Text-fig. 5). In Pongidae the protocone and protoconule

are close together, and the arms of the protocone are more widely divergent so that the protoconule stands more immediately to the mesial side of the protocone. When the protocone is situated near the lingual border, as in living apes, the protoconule is displaced towards the lingual side of the crown (Text-fig. 6).

(3) The fovea anterior is very small, with a minimal tendency to elongate transversely to the crown. Its small size is due to the position of the protoconule quite near to the base of the paracone and to the parastyle. A similar arrangement is found in tarsioids such as *Hemiacodon* and Necrolemuridae (Hürzeler, 1954*a* : 17) and must be considered primitive. In Pongidae the fovea anterior is transversely elongated, especially in modern forms in which the protoconule is displaced away from the paracone into the lingual half of the crown (Text-fig. 5).

(4) In *Oreopithecus* there is a deep Λ-shaped groove between protocone and hypocone for the reception of the entoconid. Its anterior margin is formed by the crest joining the protocone to the metaconule ; this crest is longer and directed more buccally than is normally the case in Pongidae. The posterior margin of the groove is formed by the crest which connects the hypocone to the crista obliqua near the metaconule. This crest has been regarded as a peculiarity of *Oreopithecus*, but it appears to be homologous with the " lingual marginal crest " which in Pongidae runs more directly towards the protocone, the arms of the entoconid groove having opened out (Text-fig. 5). It is probable that the condition in *Oreopithecus* is primitive in that it is associated with a markedly V-shaped protocone, well separated from the metaconule. The crest directly connecting the protocone and hypocone of Pd^4 in *Oreopithecus* is an independent formation, perhaps paralleled in the molars of Cercopithecidae.

(5) The crista obliqua, instead of passing directly to the tip of the metacone as in Pongidae, is frequently diverted in *Oreopithecus* to a cuspule situated on the antero-lingual side of the metacone. On Pd^4, however, the crista obliqua runs to the tip of the metacone, and it is probable that this is the primitive arrangement. Hürzeler (1958) is probably correct in homologising the more buccal part of the crista obliqua with the " mesial metaconule crest " of early Primates, but its connection with the tip of the metacone appears to be a very ancient character. The condition in *Oreopithecus* would therefore constitute a peculiar specialisation, perhaps associated with the elongation of the molar.

(6) *Oreopithecus* appears to lack an occlusal facet on the posterior side of the oblique crest, produced by the hypoconulid. In the Pongidae the hypoconulid is characteristically enlarged and independent, even in the Oligocene *Propliopithecus*. While a secondary reduction is possible, it seems more likely that *Oreopithecus* is primitive in this respect.

Among the Pongidae, *Oreopithecus* shows most resemblance in the upper molar pattern to *Proconsul*, *Limnopithecus* and *Pliopithecus*. This is shown by the following characters (Text-fig. 5) :

(1) Trigon basin comparatively small, owing to the vertical orientation of the cusps. This feature is also found in *Sivapithecus*. In all living Pongidae, and also in *Dryopithecus germanicus*, *D. punjabicus* and *Gigantopithecus* the trigon cusps are

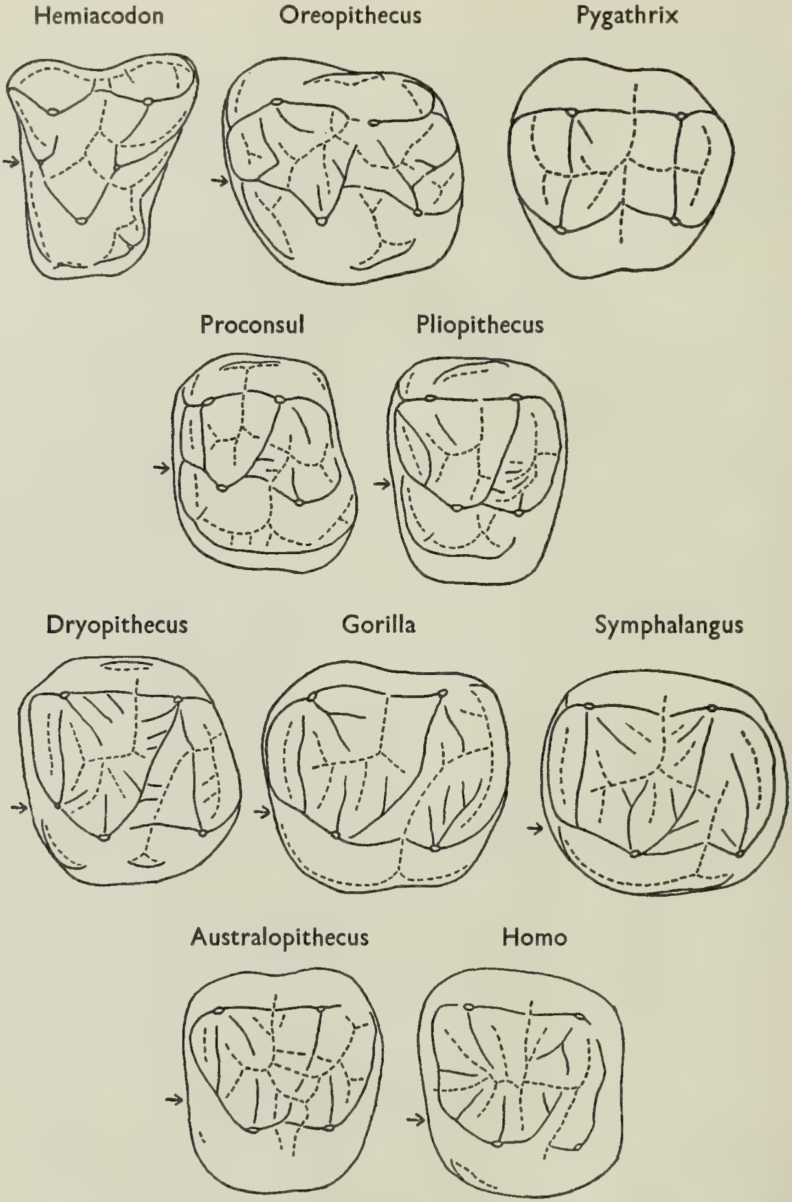
Hemiacodon
Oreopithecus
Pygathrix
Proconsul
Pliopithecus
Dryopithecus
Gorilla
Symphalangus
Australopithecus
Homo

FIG. 5. Left upper molars, drawn to the same width. *Hemiacodon gracilis*, M 10386 (M^1). *Oreopithecus bambolii*, M 11555 (M^2 restored). *Pygathrix rubicunda*, 20.12.4.3. *Proconsul africanus*, M 14085 (M^1, reversed). *Pliopithecus antiquus*, from cast (M^1). *Dryopithecus germanicus*, from cast (M^1 or M^2). *Gorilla gorilla*, 49.663 (M^2). *Symphalangus syndactylus*, 19.11.12.2 (M^2). *Australopithecus africanus*, from cast (M^1). *Homo sapiens*, Australian, Oxford Coll. Aus. 30.980 (M^1). The position of the protoconule is indicated by an arrow.

splayed apart, so that their tips are situated quite near the edges of the crown (Text-fig. 6).

(2) Cingulum strongly developed. In the remaining genera it is reduced to various degrees or even absent. When present the cingulum nearly always passes round the lingual side of the protocone in Pongidae, whereas in *Oreopithecus* it is interrupted there.

(3) Protoconule, when present, situated at the middle of the anterior border of the crown. Correlated with this, the fovea anterior is small and situated entirely on the buccal half of the tooth. This character occurs also in *Sivapithecus*. In Pongidae with widened trigons the protoconule is more lingually situated and the transverse diameter of the fovea anterior is greater (Text-figs. 5, 6).

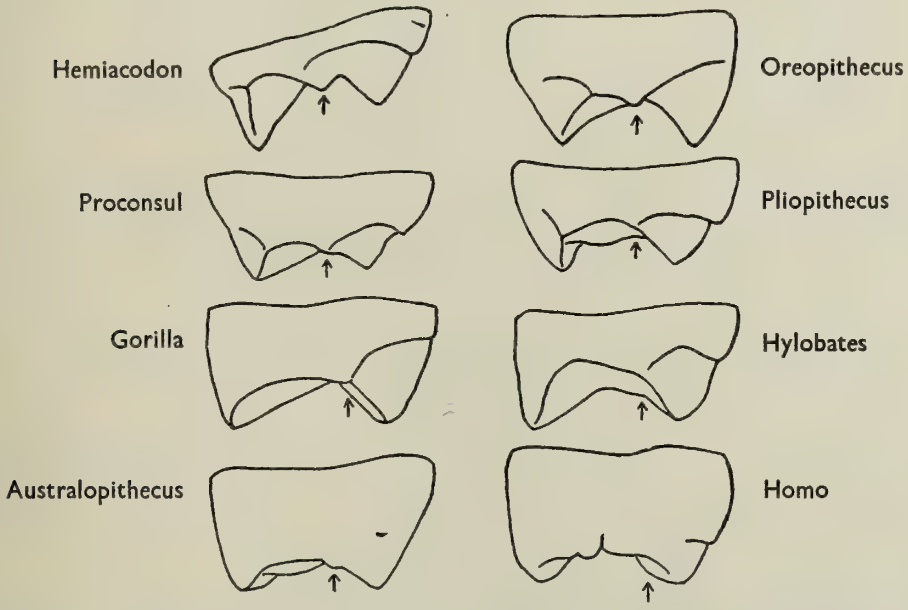

Fig. 6. Right upper molars, anterior (mesial) view. Drawn to the same width. *Hylobates hainanus*, 93.9.12.1 (M^1). *Homo sapiens*, European. Otherwise same specimens as Text-fig. 5.

(4) Paracone much higher than the parastyle, its anterior slope steeply inclined. This character is also found in the gorilla and in gibbons. At the other extreme are *Dryopithecus* and the orang (Text-fig. 7).

In its molar pattern, therefore, *Oreopithecus* appears to retain primitive features that are not known in any of the Pongidae, and at the same time it resembles what are presumably the most primitive members of the family rather than the later forms. This suggests that it is a survivor, specialised in its own way, from a prepongid stock. Some features of the lower dentition, such as the persistence of the paraconid on M_1, are consistent with this view.

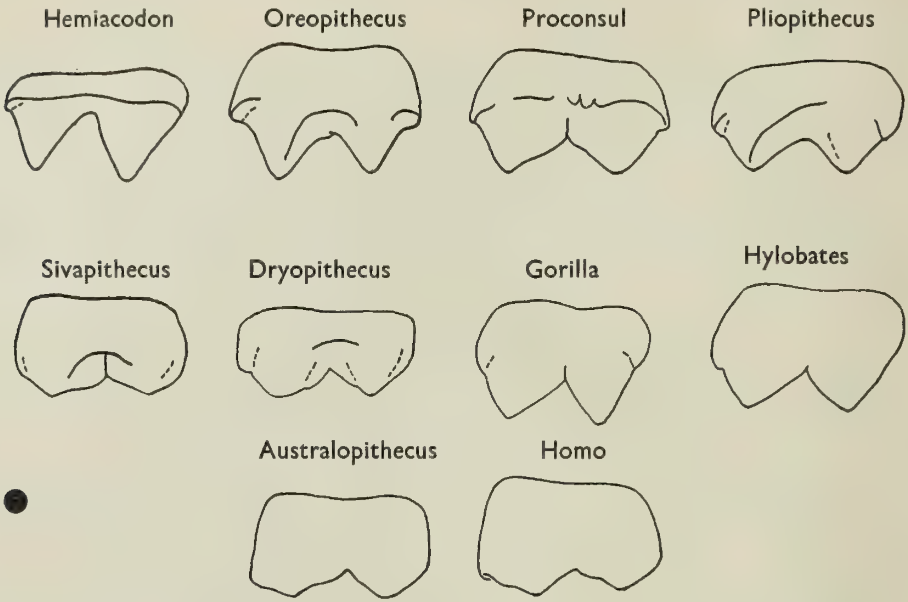
Hemiacodon
Oreopithecus
Proconsul
Pliopithecus
Sivapithecus
Dryopithecus
Gorilla
Hylobates
Australopithecus
Homo

FIG. 7. Left upper molars, buccal view. Drawn to the same length. *Sivapithecus indicus*, M 13365. *Gorilla*, 61.7.29.27. *Hylobates hoolock*, 1096*a* (M²). *Homo sapiens*, European. Otherwise same specimens as Text-fig. 5.

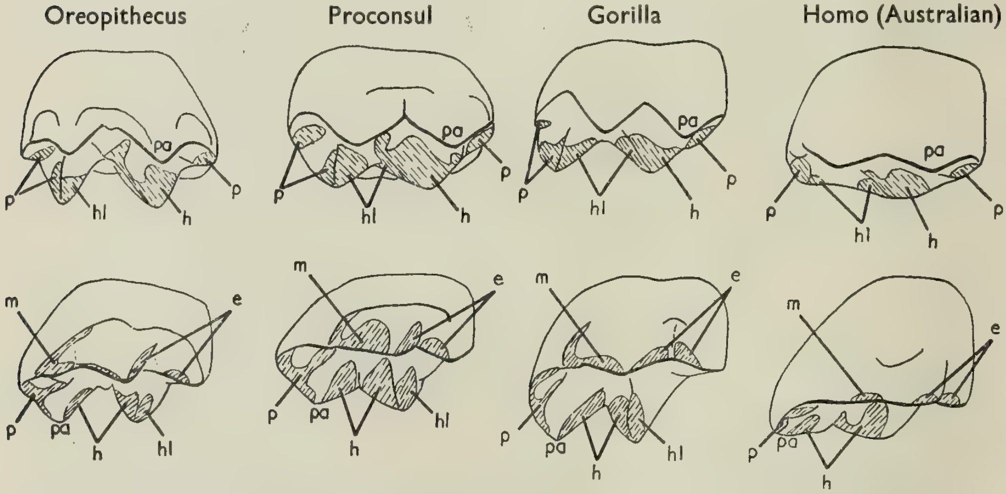
Oreopithecus
Proconsul
Gorilla
Homo (Australian)
pa
p
p
hl
h
pa
p
p
hl
h
pa
p
p
hl
h
pa
p
p
hl
h
m
e
p
pa
h
hl
m
e
p
pa
h
hl
m
e
p
pa
h
hl
m
e
p
pa
h

FIG. 8. Oblique views of right upper molars. Not to scale. In the upper drawings the teeth are seen in buccal and somewhat occlusal view, looking in the direction of the scratches made during the buccal phase of occlusion. In the lower drawings the teeth are seen in the direction of the oblique scratches made during the lingual phase of occlusion, i.e. anterolingually. *pa*, paracone. Wear facets due to the protoconid (*p*), hypoconid (*h*), hypoconulid (*hl*), metaconid (*m*) and entoconid (*e*) are indicated.

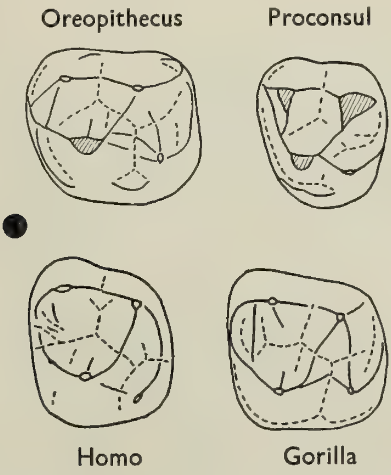
Oreopithecus
Proconsul
Homo
Gorilla

FIG. 9. Left Pd⁴, crown view. Drawn to the same width. *Oreopithecus*, M 11555. *Proconsul nyanzae*, Coryndon Museum 993, 1947. *Homo sapiens* (European), specimen supplied by Dr. M. V. Stack. *Gorilla*, 1011q.

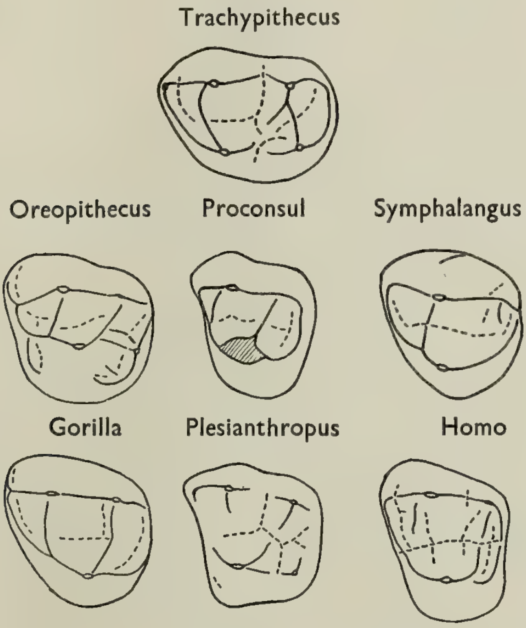
Trachypithecus
Oreopithecus
Proconsul
Symphalangus
Gorilla
Plesianthropus
Homo

FIG. 10. Left Pd³, crown view. Scale various. *Trachypithecus obscurus*, 6.10.4.3. *Oreopithecus*, M 11555. *Proconsul nyanzae*, Coryndon Museum 993, 1947. *Symphalangus*, 0.3.2.23. *Gorilla*, 1011q. *Plesianthropus transvaalensis*, after Broom & Robinson (1950). *Homo sapiens* (European), specimen supplied by Dr. D. A. Goose.

Pd^4 reflects the molar pattern, but in the relation of the crista obliqua to the metacone it shows a resemblance to the Pongidae that is often lost in the molars (Text-fig. 9). The level of molarisation of Pd^3 is greater than in most gibbons, but is much like that of *Proconsul nyanzae* (Text-fig. 10). The characteristics of the anterior part of the molar are repeated on P^4, as may be seen in the vertical, acute paracone, the V-shaped protocone, the small fovea anterior and the development of the cingulum (Text-fig. 11)

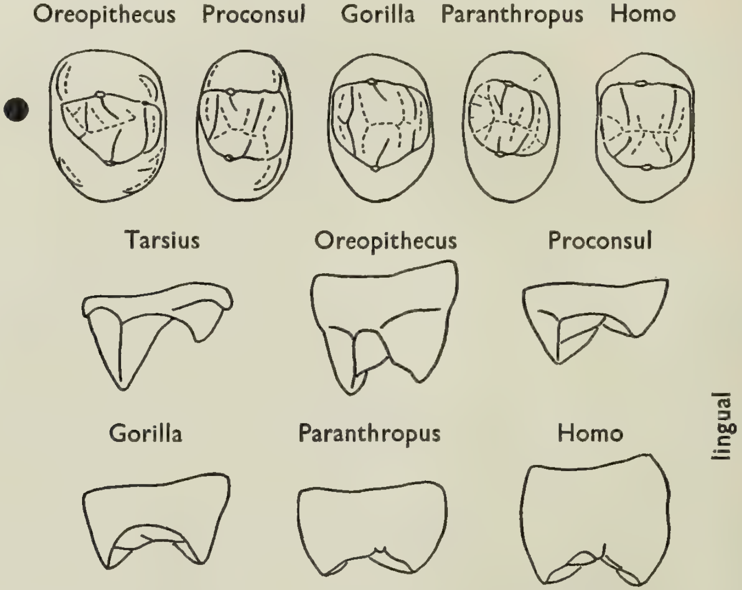

FIG. 11. Above, left P^4, crown view. Below, right P^4, anterior view. *Oreopithecus*, M 11555 (reversed in upper figure). *Proconsul africanus*, holotype (reversed in lower figure). *Gorilla*, 20.4.13.3. *Paranthropus robustus*, from cast (reversed in lower figure). *Homo sapiens*, specimen showing fovea anterior. *Tarsius spectrum*, 46.1.29.2.

The small size of the canine is a character shared with *Parapithecus*. Its shape is in all probability primitive (Remane, 1927, 1955) (Text-fig. 12); it shows much resemblance to the female canine of *Pliopithecus* (Hürzeler, 1954*a*, fig. 10). Though a precanine diastema is usually well developed in Pongidae, it is very short in the female skull of *Proconsul africanus* (Le Gros Clark & Leakey, 1951).

4. *Comparison with Hominidae.* Hominid teeth are notoriously variable, and for considerations of space it is necessary to confine attention to those features that are sufficiently frequent to be regarded as characteristic. The material studied consisted mainly of the teeth of Europeans, Australians, *Pithecanthropus pekinensis* and Australopithecinae, the last two groups seen only as casts.

Hominid upper molars show numerous differences from those of *Oreopithecus* :

(1) They are nearly always broader than long, and thus resemble the majority of Pongidae. *Oreopithecus* is specialised in the elongation of its molars.

(2) The enamel is thick. Measurements made on broken molars of man and gorilla, comparable with those made on *Oreopithecus*, are given in Table III. The effect of the thick enamel layer is to round off the crests and cusps, so that even on unworn teeth the sulci are often more conspicuous than the positive elements of the pattern. Although there are no data for Australopithecinae, it is evident from the general appearance of their crowns that they resembled *Homo* in possessing thick enamel. Thickening of enamel would increase the life of the tooth and might be an adaptation to greater longevity in man.

TABLE III

Specimen		Maximum thickness of enamel (mm.)	Crown module	Percentage enamel thickness/module
Oreopithecus (M. 11555)	M^2	0·8	8·85	9·0
	M^1	0·7	7·95 (est.)	8·8
Gorilla (23.11.29.3)	M^2	1·5	18·1	8·3
	M^1	1·2	15·75	7·6
Orang (3.62)	M^2	1·2	13·55	8·8
	M^1	1·2	13·75	8·7
Man (European) 3 different individuals	M^2	1·3	9·2	14·1
	M^1	1·3	10·5	12·4
	M^1	1·3	9·6	13·5

(3) The cusps are very low; the paracone rises only slightly above the level of the parastyle, as in *Dryopithecus* and the orang (Text-figs. 6, 7).

(4) The trigon basin is larger than in *Oreopithecus* and primitive Pongidae, but it tends to occupy a smaller proportion of the crown area than in modern Pongidae (Text-fig. 5).

(5) There is usually no buccal cingulum. The lingual cingulum is also absent or extremely rudimentary in Australopithecinae and *Pithecanthropus*, but in *Homo* a Carabelli cingulum or cusp may develop in the neighbourhood of the protocone; it tends to extend round the lingual side of the protocone as in *Proconsul*. It is possible that the Carabelli cingulum is a new development in some races of *Homo*. Loss of cingula is probably a trend of pongid evolution.

(6) The arms of the protocone are normally widely open, as in Pongidae. The posterior arm tends to run directly backwards before turning buccally, and not infrequently it is intersected by a furrow which cuts off a small cusp behind the protocone, noticed in *Pithecanthropus* by Weidenreich (1937). It is not improbable that this cusp is the lingually displaced metaconule. A similar arrangement may be found in some orangs and chimpanzees.

(7) The groove between the protocone and the hypocone for the reception of the entoconid is shallow; the hypocone tends to be connected directly with the posterior side of the protocone, as in Pongidae.

(8) The protoconule, when differentiated, stands on the lingual half of the crown

near the protocone (see Text-figs. 5, 6 and the figure of a human molar tooth-germ by Röse, 1892). In this the Hominidae in general resemble the modern Pongidae, but *Australopithecus africanus* is more primitive in that the protoconule is near the middle line. There is a fovea anterior in this form, very similar to that of *Sivapithecus*.

(9) In most Hominidae the crest which defines the fovea anterior is incomplete, so that the fovea joins with the trigon basin. The surviving buccal part of the crest, on the slope of the paracone, develops in many cases into a small cusp. Sometimes this cusp is connected not to the paracone but to the anterior marginal crest. Here another cuspule may develop, buccal to the protoconule and in the buccal half of the crown. There is a tendency to form minor crests or wrinkles perpendicular to the anterior marginal crest. In Pongidae the union of the fovea anterior with the trigon basin is not uncommon, especially on M^2 and M^3. It is especially frequent in the orang, which also shows the formation of wrinkles perpendicular to the anterior border. It seems more likely that the hominid fovea anterior has passed through a stage like that typical of Pongidae, than that it has been derived directly from the condition of *Oreopithecus*, as Hürzeler suggests (1958, fig. 25). Hürzeler fails to take into account the different positions occupied by the protoconule in *Oreopithecus* and in man.

(10) The hypocone is smaller than the protocone, and the fovea posterior is relatively small. This condition is usual in gibbons. There are sometimes indications of a metacone-hypocone crest, usually represented only by its two ends ; the buccal end tends to branch off from the crista obliqua, giving the metacone the " clover-leaf pattern " noticed by Weidenreich (1945). Union of the buccal crest of the hypocone with the crista obliqua occurs in *Limnopithecus*.

(11) The crista obliqua is frequently broken up by one or more furrows, so that the fovea posterior becomes united with the trigon basin (Weidenreich, 1945). A similar intersection of the crista obliqua occurs in *Dryopithecus darwini* (Glaessner, 1931), and according to Remane (1921) the crista frequently fails to develop in the chimpanzee, especially on M^3.

(12) When present, the crista obliqua runs to the tip of the metacone, as in Pongidae.

Thus in nearly every respect in which the hominid molar pattern differs from that of *Oreopithecus* it shows affinity to the Pongidae. Even though many of the pongid resemblances are undoubtedly the products of parallel evolution, some seem to indicate that the hominid molar has passed through a stage resembling that of primitive Pongidae. By contrast, special resemblances to *Oreopithecus* are hard to find :

(1) The cuspule which in Hominidae frequently develops lingually to the paracone, on the posterior edge of the fovea anterior, has not been observed in Pongidae. Whether it is homologous with the cuspule that develops in a similar position in *Oreopithecus* is doubtful, and little weight can be given to this resemblance.

(2) The neck of the tooth is higher than in Pongidae (Text-figs. 6, 8). This again is of little value in assessing relationships : hypsodonty is a very common adaptation in mammals to severe or prolonged wear of the teeth, and within the Pongidae the

height of the crown shows considerable variation (it is higher, for example, in *Sivapithecus indicus* than in *S. africanus*).

The milk molars and premolars, reflecting the molar pattern in various ways, repeat the distinguishing characters noted in the molars (Text-figs. 9–11). Thus Pd^4 of Hominidae is less elongated, its cusps are blunter, the paracone and protocone are more widely separated, the cingulum is absent (except sometimes the Carabelli cingulum), and the fovea anterior is frequently united with the trigon basin. The same may be said of the premolars. Pd^3 is more highly molarised in that the metacone is nearly always distinct; in *Homo* the hypocone, however, is more rudimentary than in *Oreopithecus*.

The canines differ markedly in shape (Text-fig. 12). The hominid canine is peculiar among Primates in that the basal part of the crown is elevated and the cusp is blunt and comparatively low, so that the mesial and distal shoulders, which correspond to the parastyle and metastyle of the cheek teeth, are situated relatively high on the crown (Remane, 1927). Thus the canine has become modified in the same direction as the cheek teeth. In *Oreopithecus*, as in typical Primates, the upper and lower canines are interlocking: the lower canine slides in front of the upper, producing a nearly vertical wear facet. In Hominidae the plane of contact is nearly horizontal, so that the canines meet edge to edge in the manner of incisors. In conformity with the shape of the upper canine, the embrasure between the lower canine and P_3 is very shallow in Hominidae (Text-fig. 13).

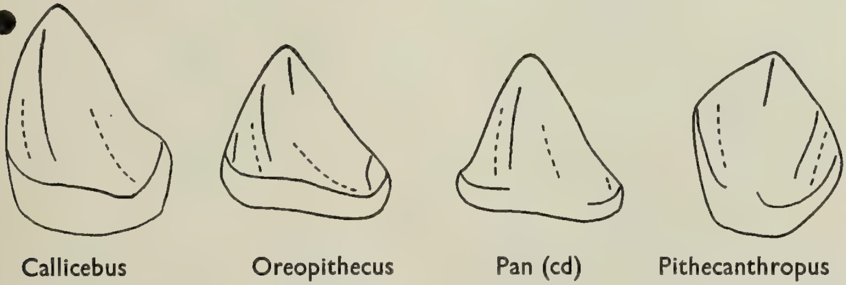

FIG. 12. Left upper canine, lingual view. Drawn to the same mesodistal length. *Callicebus leucometopa*, 27.11.1.9. *Oreopithecus*, M 11555 (reversed). *Pan*, milk canine, 48.438. *Pithecanthropus pekinensis*, from cast.

A small canine in Primates is usually associated with a short face. As the jaw swings medially, the lower canine in most Primates passes between the upper canine and I^2 (Text-fig. 14). When the face is long the canine can be large, for the incisors can be carried anteriorly to the upper canine so as to leave a diastema in which the lower canine can move. In short-faced Cebidae and Semnopithecinae, and probably also in *Parapithecus*, the lower canine is small enough to pass through the notch between I^2 and the upper canine, even though the diastema may be absent. In Hominidae the premaxilla is particularly short, and the upper incisors are situated more or less between the canines; the lower canine, instead of passing behind the incisors, travels along the incisor row. This is possible because not only has the canine become reduced in size but its shape has been modified to permit it to bite against the edge of I^2 in the manner of an additional incisor. In *Oreopithecus* the face is also greatly shortened and the canine reduced in size, but it appears to function in a different way. To judge from I.G.F. 4332, I^2 is a reduced, conical tooth, placed at a higher level than the other teeth, and the lower canine passes below it without touching it (Text-fig. 13). Hürzeler's figure of a worn lower canine (1949, figs. 8, 9) shows a large wear facet on the posterior side, due to the upper canine, but no anterior wear which might be due to I^2. Thus whereas both *Oreopithecus* and the Hominidae have developed to an extreme degree a common primate trend of shortening of the anterior part of the face, they have adapted the dentition to this change in different ways : *Oreopithecus* by sacrificing the canine-I^2 contact, while retaining the interlocking relation of the canines, the Hominidae by losing the interlocking relation and developing an incisal relation between the lower canine and I^2.

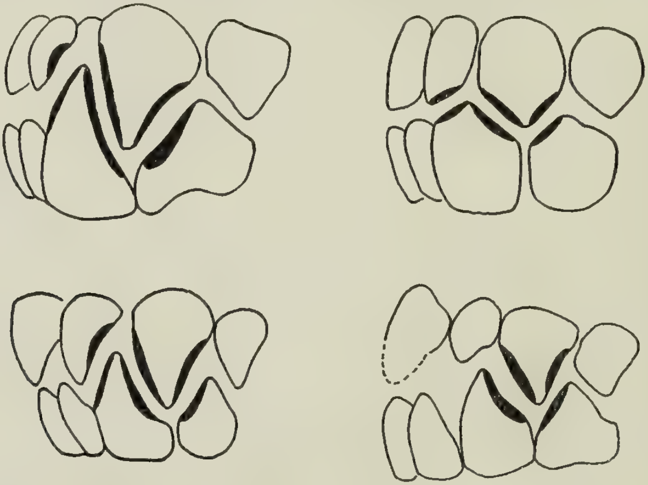

FIG. 13. Diagram to illustrate the interrelations of the anterior teeth. Position of wear facets due to upper and lower canines shown in black. Above, left, typical pongid. Above, right, hominid. Below, left, primitive primate arrangement. Below, right, *Oreopithecus*.

As Remane (1955) has pointed out, the development of the metaconid on P_3 is not a character on which far-reaching phylogenetic conclusions can be based. In man this cusp is normally weaker on P_3 than on P_4 and is quite frequently very small. Its development is not closely correlated with a reduction of the upper canine, though when P_3 is specialised as a sectorial tooth the metaconid is small or absent. Its function is to extend in a lingual direction the surface which shears against the protocone of P^3 during transverse movements of the jaw. When P_3 is not highly specialised in a sectorial direction, it is not hard to conceive that the metaconid, already well developed on P_4, could by a slight extension of the molarisation field develop also on P_3, thus increasing the chewing surface.

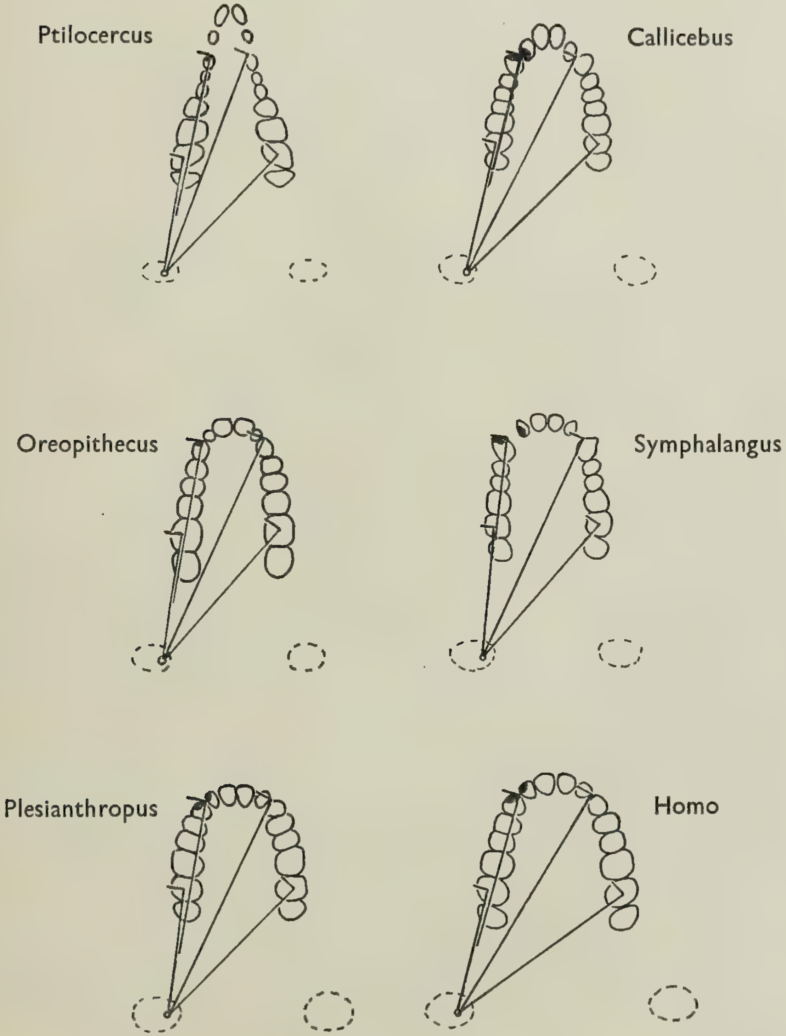
Ptilocercus
Callicebus
Oreopithecus
Symphalangus
Plesianthropus
Homo

FIG. 14. Upper dental arch and position of glenoid cavities in a number of Primates, to show direction of movement of various parts of the lower dentition when the mandible rotates round a centre in the right condyle. Wear facets produced by the right lower canine are shaded. The drawing of *Oreopithecus* is a hypothetical reconstruction.

In view of the lack of other evidence for relationship, it is probable that the similarity between *Oreopithecus* and *Paranthropus crassidens* in the proportionate lengths of the teeth (Hürzeler, 1954) is mainly coincidental. The small size of the canine has already been discussed. That P_3 is shorter than P_4 is probably a correlate of the small upper canine : in Pongidae P_3 is elongated as a sectorial tooth. That M_1 is smaller than M_2 is probably a primitive character, common in Pongidae. The enlargement of M^3 and M_3 appears to be a specialisation of *Paranthropus*, paralleled not only in *Oreopithecus* but in *Proconsul nyanzae* and many Cercopithecidae.

IV. CONCLUSIONS

Hürzeler (1958) has already reviewed the various opinions on the systematic position of *Oreopithecus*, and it is unnecessary to repeat them here. As a result of the recent discovery of new material, a much more adequate knowledge of its osteology is to be expected in the near future, and no doubt a clearer picture of its relationships will emerge. The dentition however is already better known than that of most fossil Catarrhina, and while fully recognising the dangers of relying too much on a single system of organs, the authors believe that certain conclusions may confidently be drawn from its study.

Oreopithecus does not fall within the range of any of the three living families of Catarrhina. In spite of its relatively late appearance in the geological record, it possesses a number of primitive characters that it shares with tarsioids. In the upper molars these include the high crown-relief, the V-shaped protocone, the well-developed conules, the clearly differentiated cingulum, and the small fovea anterior ; in the lower dentition the paraconid of M_1 and the weakly differentiated hypoconulid of M_1 and M_2 are probably primitive. At the same time *Oreopithecus* has become specialised in a number of ways : the face is very short, and the canines are probably smaller than in ancestral Catarrhina ; the molars are elongated, with large hypocone and fovea posterior, and a peculiar relation of the crista obliqua to the metacone ; M^3 is comparatively large, and M_3 has a well-developed " third lobe " ; P^4 has only one buccal root, and P_3 has a distinct metaconid. These specialisations have presumably developed since *Oreopithecus* separated off from the common catarrhine stock.

This peculiar combination of primitive and specialised characters seems to indicate that *Oreopithecus* is the terminal form of an independent phyletic line which extended back probably into the Oligocene. Its independence would be best expressed taxonomically by placing it in a monotypic family, Oreopithecidae, as was done by Schwalbe (1916).

On the assumption that the Catarrhina is a monophyletic group, it is necessary to believe that, probably in early Oligocene time, it bifurcated into the Cercopithecoidea and Hominoidea (in the sense of Simpson, 1931), for in the early Miocene the Cercopithecidae and Pongidae were clearly distinct, and there is evidence that the separation continued back into the Oligocene. The bilophodont molar pattern of the cercopithecoids was acquired early in their evolution, while the hominoids remained more primitive in such features as the crista obliqua. In this respect

Oreopithecus falls into the hominoid group, a position which is supported by other characters of the molar pattern that it shares with the more primitive members of the Pongidae. Thus far Hürzeler (1949) may be followed.

The present study, however, gives no support to Hürzeler's further opinion (1954, 1956, 1958) that *Oreopithecus* is especially related to the Hominidae. Kälin (1955), following Hürzeler, divides the hominoids into two branches (given superfamily rank), believed to be separate since the Oligocene. The main distinguishing characters are the size of the canine, the diastema, the form of P_3 and the shape of the dental arch, all of which are related functionally to the length of the face. One would have expected *Oreopithecus* to show evidence of hominid relationship in parts of the dentition less affected by facial shortening, such as the molars, but in these the Hominidae on the contrary approach the Pongidae and differ more or less markedly from *Oreopithecus*. Even in the canine region there are differences which suggest that reduction of the canine and associated changes have taken place independently and have not followed exactly the same course in the two groups.

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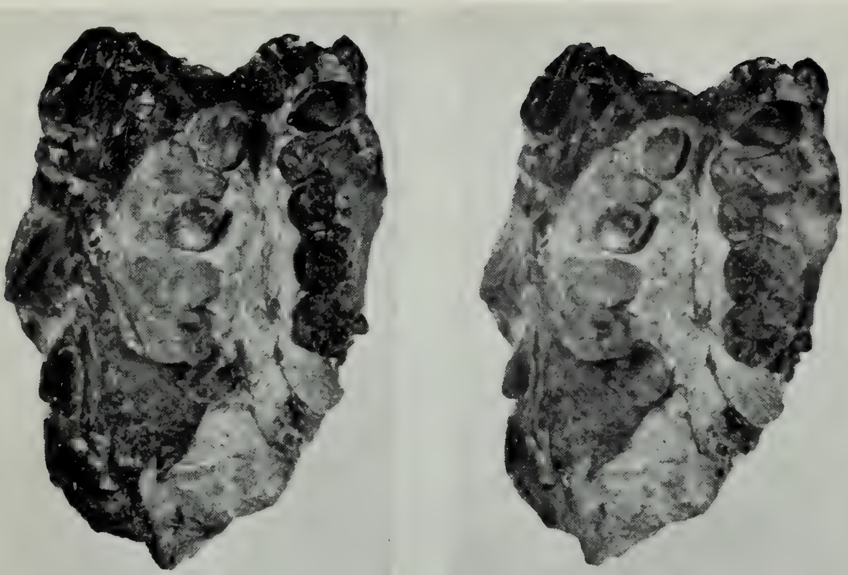
PLATE 1

Oreopithecus bambolii (M 11555)

Fig. 1. Stereophotographs of the specimen seen in palatal view. Natural size.
Fig. 2. Left side view. × 2.

1



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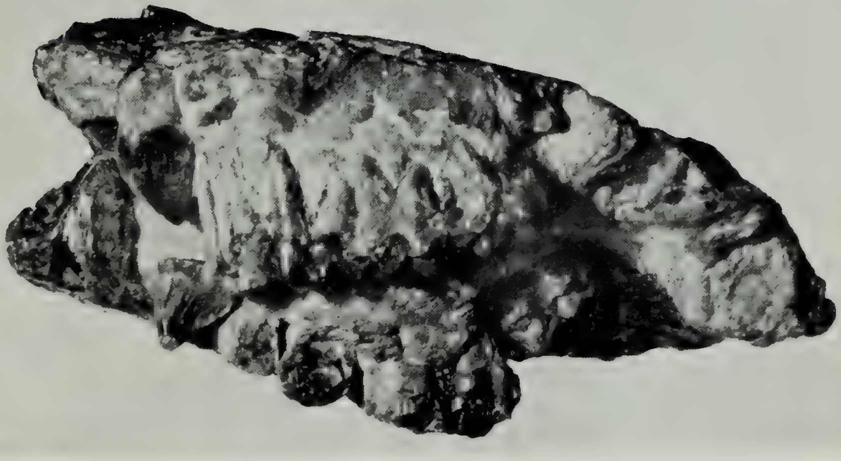

BEETLES FROM THE LONDON CLAY (EOCENE) OF BOGNOR REGIS, SUSSEX

E. B. BRITTON

BRITISH MUSEUM
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BEETLES FROM THE LONDON CLAY (EOCENE) OF BOGNOR REGIS, SUSSEX

By E. B. BRITTON

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SYNOPSIS

A systematic account is given of 231 specimens of fossil beetles collected from the beach at Bognor Regis, Sussex, by Mr. E. M. Venables and Mr. H. E. Taylor. The beetles are the first insects to have been obtained from the London Clay, and represent the families Anobiidae, Eucnemidae, Throscidae, Scolytidae, Curculionidae and Scarabaeidae. Eight new genera and eleven new species are described. In addition there are some 47 other forms, but their state of preservation precludes adequate description. Two new species are referred to modern genera, one of which, *Pactopus* (family Throscidae), is represented by one living species occurring in British Columbia and the north-west United States. Almost all of the beetles belong to groups of which the living forms feed in, or are associated with, wood or bark.

I. INTRODUCTION

For many years two well-known amateur geologists, Mr. H. E. Taylor and Mr. E. M. Venables, have collected fossils from the London Clay from the beach at Bognor Regis, Sussex. Among their discoveries are many pyritized beetles which are the first insects known from the London Clay.* The specimens are found in the intertidal zone, where they are washed out of the matrix by the action of the sea. No specimens have, as yet, been found *in situ*. Details of the method of collecting will be given in a separate paper by Messrs. Venables & Taylor.

The beetle remains are very small, always less than 6 mm. in length, so that their recognition amongst the beach detritus calls for very keen observation. Nevertheless, the skill and sustained enthusiasm of the collectors has resulted in an accumulation of no less than 231 specimens. Of these 119 specimens were collected by Mr. Taylor and 112 by Mr. Venables. Both Mr. Venables and Mr. Taylor have now generously presented their collection to the British Museum (Natural History), and the numbers given throughout the text are the registered catalogue numbers of the Department of Palaeontology, British Museum (Natural History).

The 231 specimens represent some 58 forms in seven families, namely, Anobiidae, Eucnemidae, Throscidae, Scolytidae, Carabidae, Scarabaeidae and Curculionidae, the latter greatly predominating. The Curculionidae (Weevils) is also the dominant family in the Recent fauna, being the largest in the Animal Kingdom and numbering 60,000 known species.

In some cases the specimens can be assigned to a family with certainty. Less frequently the subfamily or tribe is recognizable, but in only two cases is it possible to place the specimen in an existing, modern genus. I have thought it advisable to erect new genera for those species which can be classified to a subfamily for the following reasons : (*a*) It is desirable that names should be provided in this, the starting point of a new beetle fauna, and (*b*) it is a mistake to attempt to force the new species into the framework of existing genera when the evidence available is insufficient. This practice would imply a certainty that did not, in fact, exist.

The collection provides some positive information on the insect fauna of the Eocene. It is hoped that the knowledge that insect fossils are to be found in the London Clay at Bognor may lead to the discovery of similar remains in exposures elsewhere.

---

* The first beetles were discovered by Mr. Venables in May, 1936. Mr. Taylor started his collection in 1951.

II. OBSERVATIONS ON HABITAT

The maximum thickness of the London Clay is about 500 ft., and all evidence points to its having been deposited in the sea beyond the mouth of a great river. With this in mind it is of interest to observe that most of the species of Coleoptera found at Bognor belong to groups of which the modern forms feed upon, or are associated with, wood or bark. Of the families represented in the collection, the Anobiidae, Eucnemidae, Throscidae and Scolytidae, are composed very largely of species found in wood or bark. In addition, most of the species representing the Curculionidae belong, where recognizable, to groups which at the present time have a wood-feeding habit. Even one of the two species of Scarabaeidae belongs to a tribe, representatives of which are found in decaying wood.

Fossil wood is commonly found at Bognor and at other coastal exposures of the London Clay. It might be thought likely that beetles would be found in this wood, but Mr. Taylor has informed me that although he has examined quantities of the wood he has never found an insect in it.

The London Clay beetles show no unusual or primitive characters when compared with modern forms. This is to be expected as it is well established that the origins of the families of Coleoptera were very remote.

The distributions of the modern species most closely related to the fossil forms are very diverse, so that it is scarcely possible to generalize on the likely climatic conditions in which the fossil species lived. Such indications as there are suggest that the climate was Mediterranean or subtropical. Information on the distribution of related forms is given with the descriptions of the individual genera or species.

III. SYSTEMATIC DESCRIPTIONS

Order COLEOPTERA

Family ANOBIIDAE Redtenbacher, 1849

Genus *VENABLESIA* nov.

DIAGNOSIS. Antennal insertions not close ; eye not divided by the canthus ; posterior angles of the pronotum obtuse and with a small shallow emargination at the apex of each ; metasternum transverse with a median longitudinal groove ; elytra with a scutellar striole ; anterior and middle legs when retracted fit into a transverse cavity between the posterior edge of the prothorax and the anterior edge of the metasternum ; basal abdominal ventrite hollowed to receive the transverse posterior coxa and the coxa hollowed posteriorly to receive the trochanter and the femur ; all legs can be retracted to conform to the general level of the ventral surface.

TYPE SPECIES. *Venablesia colluvium* sp. nov.

DESCRIPTION. The prothorax is excavate beneath and hooded over the head which is deflexed so that it rests on the flat anterior faces of the anterior coxae ; the antennae when at rest are received into a cavity in the prosternum between the anterior coxae, the cavity between the eye, mandible and anterior tibia on each side being filled by the enlarged basal segment of the antenna ; eyes large, partly covered by the edge of the prothorax with a canthus projecting on to the eye from the inner side above the basal segment of the antenna ; mandibles large and flat ; metasternum transverse, with a median longitudinal groove ; anterior and middle legs retractable into a transverse cavity between the posterior edge of the prothorax and the anterior edge of the metasternum, the coxa, tibia and tarsus of the middle leg being visible when retracted ; basal abdominal ventrite is hollowed to receive the transverse posterior coxa ; the coxa is hollowed posteriorly to receive the trochanter and femur so that when retracted the lower surface of the posterior leg, like the other legs, conforms with the general level of the lower surface ; the metasternum terminates anteriorly in a pointed peg-like process ; the second and fifth abdominal ventrites are visible ; elytra each with nine longitudinal, punctured striae and a short striole at the base on the inner side of the inner stria ; a very small scutellum is visible between the elytra at the base ; the outer elytral stria is rather more deeply impressed than the remainder ; the pronotum has a small shallow emargination at the apex of the posterior angle on each side ; sutures between abdominal ventrites are more deeply impressed at the sides than in the middle.

REMARKS. The gender of the generic name is feminine. The genus is named in honour of Mr. E. M. Venables to whom we owe the discovery of the specimens on which this genus is based.

Venablesia colluvium sp. nov.

(Pl. 2, figs. 1, 3)

DIAGNOSIS. As for genus.

TYPE MATERIAL. *Holotype:* In.49102. A specimen with prothorax and hindbody, with elytra, but without head. *Paratypes:* Twenty-five specimens. In.49103–49106, with head, pronotum and hindbody. In.49107–49109, In.49393–49395, with part of pronotum and hindbody. In.43364, In.49110–40113, In.40396–49403, In.49429, In.49434, with hindbody only.

MEASUREMENTS. Length ; from apex of prothorax to apex of abdomen, 2·1–4·0 mm.

DESCRIPTION. Elytra with striae impressed and punctured, the punctures separated by less than their own diameter ; elytral intervals between striae with sparse, minute punctures ; pronotum, metasternum and abdominal ventrites closely punctured ; wings fully developed.

REMARKS. The hooded form of the prothorax, the deflexed head, posterior angles of the pronotum obtuse, the hollowed first ventrite, antennae not inserted close together, the eye not divided by the canthus and the elytra with a scutellar striole place the genus in the family Anobiidae, very close to the modern genus *Stagetus* Wollaston (= *Theca*, Mulsant & Rey). The ventral surface of *Stagetus denticornis* Champion, an Indian species, is illustrated in Pl. 2, fig. 2, for comparison with *Venablesia*. The pronotum differs from that in *Stagetus* by having a small, shallow emargination at the junction of the lateral and posterior edges.

The genus *Stagetus* is widely distributed but the majority of the 54 described species occur in the southern parts of the palaearctic region. No species of the genus are found in the British Isles, although several species occur in France. As far as is known the species of *Stagetus* live in woody fungi (e.g. *Fomes*).

The specific name is derived from *colluvium* = detritus.

Venablesia spp. indet.

Specimen In.49430, including head; thorax and abdomen, but badly worn. Length 2·5 mm.; greatest width (across elytra at the level of the metasternum) 2·25 mm. Prothorax hooded over the head, which is deflexed and resting on the prosternum. Legs folded into transverse cavities as in *Venablesia*. Metasternum transverse, with a deep median longitudinal groove. Anterior edge of its metasternum between the globular middle coxae broadly V-shaped, open anteriorly.

Specimens In.49431–49432, including prothorax and hindbody. Length 2·25 mm., and 1·65 mm.; greatest width 1·6 mm. and 1·25 mm. The part of the prothorax visible in the smaller specimen suggests the hooded form of Anobiidae. Legs folded into transverse cavities. Metasternum transverse with a median longitudinal groove and a narrow anterior process between the middle coxa.

Family THROSCIDAE Erichson, 1847

Subfamily THROSCINAE Erichson, 1847

Genus ***PACTOPUS*** LeConte, 1868

DIAGNOSIS. Throscidae in which the second and third abdominal ventrites have a longitudinal groove on each side for the reception of the posterior tarsi; metasternum with a similar narrow but more oblique groove on each side for the reception of the tarsi of the middle legs.

TYPE SPECIES. *Pactopus horni* LeConte, 1868.

Pactopus avitus sp. nov.

(Pl. 2, fig. 4; Pl. 3, fig. 1)

DIAGNOSIS. Species of *Pactopus* in which the striation of the elytra and the punctuation of the pronotum and abdomen are very faint.

TYPE MATERIAL. *Holotype:* In.49404.

MEASUREMENTS. Length 6·2 mm.; maximum width, at the posterior angles of the pronotum 2·5 mm.; length of the elytra 4·5 mm.; length of the pronotum 1·4 mm.

DESCRIPTION. The single specimen can be assigned with certainty to the family Throscidae, and to the subfamily Throscinae. The following characters of the family are clearly visible: general "elateroid" form; prothorax markedly tapered towards the anterior end; head sunk into the prothorax as far as the middle of the eyes ; antennae long, inserted on the frons before the middle of the eyes, and retracted into deep grooves on the underside of the prothorax ; the suture between the first two abdominal ventrites not obliterated ; prosternum truncate in front and produced posteriorly into a process which fits into a median cavity in the anterior end of the mesosternum ; head with the labrum visible above the mandibles which rest behind on the truncate end of the prosternum ; posterior angles of the pronotum acute ; elytra covering the abdomen.

REMARKS. The subfamily Throscinae is distinguished from the subfamilies Lissominae and Balginae[1] by the following characters which are all visible in the specimen : trochanters short (ratio of length of middle femur/length of the trochanter c. 3 : 1) ; anterior end of the prosternum transversely truncate, not convex ; the antennal groove in the propleuron on each side is open (i.e. does not communicate with a pocket) and extends back along the suture between pleuron and sternum, then curves outwards until it runs close to the lateral edge of the prothorax near the posterior angle.

The genus *Pactopus* differs from all other known genera in the family by having longitudinal grooves on the second and third ventrites for the reception of the posterior tarsi. In addition the tarsi of the middle legs are received into narrow oblique grooves on the metasternum. The presence of grooves on the abdomen for the reception of the posterior tarsi is rare in Coleoptera, occurring elsewhere only in the subfamily Gastraulacinae, of the family Eucnemidae, and in *Octocryptus* and *Hexaulacus* of the Elateridae[2]. The available characters of the specimen do not diverge in any important degree from those of the only known living species, *Pactopus horni* LeConte, and for this reason I have no hesitation in including the London Clay specimen in the same genus. The ventral surface of *Pactopus horni* is illustrated in Pl. 3, fig. 2, for comparison with *Pactopus avitus*.

Pactopus avitus differs from the modern species *P. horni*, by having the elytral striation, and puncturation of the pronotum and abdomen very faint.

Pactopus horni LeConte is found in northern California, Nevada, Oregon, Washington, Vancouver and British Columbia. No information on the habitat of the species is available, but it probably lives in rotten wood, like other Throscidae.

The specific name is derived from *avitus* = ancestral.

Family EUCNEMIDAE Bach, 1854

Subfamily GASTRAULACINAE Fleutiaux, 1901

Genus ***POTERGITES*** nov.

DIAGNOSIS. An Eocene genus of Eucnemidae ; propleuron on each side has a groove along the outer margin for the reception of the antenna ; metasternum with an oblique groove on each side for the reception of the middle tarsus ; second and third abdominal ventrites with a groove on each side for the reception of the posterior tarsus ; lateral edges of the pronotum broadly rounded, posterior angles acute ; basal edge of the pronotum with a truncate lobe in the middle ; scutellum transverse, quadrate ; elytra each with nine longitudinal striae ; mesosternum with a median anterior cavity for the reception of the posterior process of the prosternum ; posterior coxae transverse, with a posterior hollow for the reception of the femur ; abdomen with five visible ventrites.

---

[1] Crowson, R. A., 1955, The Natural Classification of the Coleoptera : 63.

[2] Fleutiaux, E., 1942, Revue française d'Entomologie, **9** : 79, 10 figs. Moyens de Défense de quelques Coléoptères Sternoxes.

TYPE SPECIES. *Potergites senectus* sp. nov.

REMARKS. The genus is placed with certainty in the family Eucnemidae and the subfamily Gastraulacinae because of the body size and form and presence of the grooves for the reception of the antennae and the mid and hind tarsi.

The subfamily Gastraulacinae has been divided by Fleutiaux into two tribes, the Gastraulacini and the Dendrocharini, each of which contains one genus in which both metasternum and abdomen have grooves for the tarsi. The Gastraulacini have the mandibles exposed from below, while in the Dendrocharini they are covered by the prosternum. The head is missing in all specimens available so that it is not possible to place the present genus with certainty either with *Potergus* in the Dendrocharini or with *Epipleurus* in the Gastraulacini. The form of the pronotum, however, suggests that it is more closely related to *Epipleurus*. *Epipleurus* and *Potergus* each include a single living species and both occur in the Indo-Malayan region.

The gender of the generic name is masculine.

Potergites senectus sp. nov.

(Pl. 3, figs. 3, 4)

DIAGNOSIS. As for genus.

TYPE MATERIAL. *Holotype :* In.49405. A specimen with mesothorax and hindbody attached but without elytra. *Paratypes :* Ten specimens, In.49406–49415, hindbody only, one with elytra ; 14 specimens, In.49114–49125, 49689–49690, hindbody only, five with elytra.

MEASUREMENTS. *Holotype :* length (pronotum and hindbody) 3·0 mm. *Paratypes,* length (mesothorax, metathorax and abdomen) 1·9–3·2 mm.

DESCRIPTION. Pronotum : ratio of width across the posterior angles to the middle length 1·6 : 1. Elytra : width across the base equal to the middle length. The sides of the pronotum are broadly rounded anteriorly and the posterior angles are acute. Surface of the pronotum densely punctured, the punctures separated by less than their own diameter. The grooves for the reception of the antennae run from the anterior edge of the pronotum parallel to the lateral edge, the grooves being deepest at the anterior end. The surface of the scutellum bears 6 or 7 punctures like those on the pronotum. The elytral striae are marked by fine regular punctures. Surface of the metasternum densely punctured, with the oblique tarsal groove directed from the middle coxal cavity towards the posterior outer angle. Abdominal ventrites densely punctured.

REMARKS. The specific name is derived from *senectus* = very old.

Family SCARABAEIDAE W. S. Macleay, 1839

Subfamily APHODIINAE W. S. Macleay, 1839

Tribe EUPARIINI Schmidt, 1910

Genus *SAPROSITES* Redtenbacher, 1858

DIAGNOSIS. A genus of Aphodiinae in which the middle and posterior tibiae are without transverse carinae ; coxae of the middle legs approximately cylindrical with the axis inclined about 60° to the longitudinal axis of the body ; posterior coxae flat, extending the full half-width of the metasternum ; metasternum with a deep, median longitudinal groove ; mesosternum with a median longitudinal ridge ; abdomen with six ventrites visible (at the sides) each ventrite being deeply, longitudinally strigose along the base.

TYPE SPECIES. *Saprosites peregrinus* Redtenbacher 1858 (by monotypy).

Saprosites cascus sp. nov.

(Pl. 4, fig. 1)

TYPE MATERIAL. *Holotype :* In.49695. *Paratypes :* Three specimens, In.49496, In.49427–49428.

MEASUREMENTS. Length *c.* 2·6 mm.; width *c.* 1·7 mm. (mesothorax, metathorax and abdomen).

DESCRIPTION. Metasternum coarsely punctured, the punctures most numerous near the anterior and lateral margins ; abdominal ventrites densely and coarsely punctured towards the sides, punctures absent or sparse in the middle ; each ventrite with a transverse row of rather quadrate punctures along the anterior margin, the punctures separated by narrow ridges, giving the longitudinally strigose appearance ; elytra with longitudinal punctured striae ; median longitudinal ridge between the middle coxae itself with a very fine median longitudinal groove which is continued on to the metasternum to unite with the deep median groove.

REMARKS. The genus *Saprosites* is represented by about 50 living species which are mainly tropical in distribution. It occurs in tropical America, Central Africa, Madagascar, India, Indo-China, Borneo, New Guinea, Australia, New Zealand and Hawaii. Very little is known of the biology of the species of *Saprosites*, but some, at least, are known to live beneath the bark of dead trees.

The specific name is derived from *cascus* = old.

Subfamily SCARABAEINAE W. S. Macleay, 1839

Genus *ONTHOPHAGUS* Latreille, 1802

DIAGNOSIS. Metasternal shield broad, with longitudinal, cylindrical middle coxae ; posterior coxae transverse, abdomen small ; without visible scutellum ; elytra with six punctured striae which are deepened at their apices.

TYPE SPECIES. *Onthophagus taurus* (von Schreber).

Onthophagus sp. indet.

MATERIAL. One specimen, In.49691, comprising mesosternum, metasternum, abdomen and cast of elytra.

MEASUREMENTS. Length 1·6 mm.; maximum width 2·0 mm.

REMARKS. The combination of broad metasternal shield, longitudinal middle coxae, transverse posterior coxae; small abdomen and elytral striae deepened at their apices places this specimen with reasonable certainty in the genus *Onthophagus*. This is one of the largest of animal genera, including about 2,000 living species, of which most are dung-feeders, though some are found in carrion and others in fungi or decaying vegetation.

Family SCOLYTIDAE Stephens, 1839

Genus ***BLASTOPHAGUS*** Eichoff, 1864

?***Blastophagus*** sp. indet.

MATERIAL. One specimen, In.49416, including head, pronotum, elytra, abdomen. One antennal club and scape and one posterior femur are visible.

MEASUREMENTS. Length 4·15 mm. (including head).

DESCRIPTION. Form cylindrical; head with a short blunt rostrum, antenna terminated in a compact, broadly expanded, four-segmented club, basal segment (scape) half as long as the antenna; the two basal abdominal ventrites each longer than the third and fourth ventrites together; posterior coxae transverse; basal edge of the metasternum having an anteriorly directed median angle continued into a short median groove; metasternum punctured; middle coxae globular, separated by less than their own width; anterior coxae globular, almost contiguous; posterior femur fusiform, ratio length/width = 3 : 1; pronotum with faint traces of puncturation, without defined lateral margins; elytra with striae slightly impressed but regularly and coarsely punctured.

REMARKS. The specimen differs from *Blastophagus* in having the eyes more nearly circular, and lacking the granulate carina along the basal edges of the elytra. *Blastophagus* is represented in the British fauna by two living species which live beneath the bark of pine trees. *Blastophagus piniperda* (Linnaeus) is figured in *Handbooks for the Identification of British Insects*, **5**, part 15, 1953, E. A. J. Duffy, fig. 34.

Family CURCULIONIDAE Gyllenhal, 1813

Subfamily HYLOBIINAE Thompson, 1865

Genus ***PISSODITES*** nov.

DIAGNOSIS. Mesothorax with globular coxae separated by very narrow median extensions of the mesosternum and metasternum, the distance between the coxae being about one-eighth of the diameter of the coxae; posterior coxae transverse, each with ratio of width/length about 1·8 : 1; posterior coxae separated by about half the width of a coxae; metasternum ratio, greatest width/middle length about 1·5 : 1; metasternum separated from the first abdominal ventrite by an obtuse angled suture; the first and second abdominal ventrites very large, each about as long as the third, fourth and fifth ventrites together, scutellum visible, triangular.

TYPE SPECIES. *Pissodites argillosus* sp. nov.

REMARKS. The generic name is masculine and is derived from *Pissodes*, a genus of living weevils.

Pissodites argillosus sp. nov.

(Pl. 4, figs. 3, 4)

DIAGNOSIS. As for genus.

TYPE MATERIAL. *Holotype:* In.49325. *Paratypes:* Eight specimens, In.49326–49333. The specimens comprise the hindbody and elytra only.

MEASUREMENTS. Length 2·4–3·2 mm.; width 1·3–1·9 mm.

DESCRIPTION. Ventral surface, metasternum and the first and second ventrites fairly uniformly punctured, the density of punctures being *c.* 350 per sq. mm. Ventrites 3, 4 and 5 are rather more densely and coarsely punctured. Suture between the first and second ventrites usually slightly arched, faint in the middle and strongly impressed at the sides. Posterior margins of the coxal cavities usually very narrow and slightly raised, defined by a row of larger semi-confluent punctures parallel to the edge of the cavity. From the apex of the median posterior angle of the metasternum a short median groove extends forwards about 0·4 mm. and ends in the middle of a shallow elliptical depression. Each elytron with 10 striae, each of which is a shallow longitudinal groove with about 36 deep punctures distributed along it, the punctures near the base spaced by less than their own width.

REMARKS. The species should be easily recognizable by its slender form and dense puncturation. A photograph of the ventral surface of the living species *Pissodes castaneus* Degeer has been included (Pl. 4, fig. 2) for comparison with *Pisssodites*. The larvae of the species of both *Pissodes* and *Hylobius* feed in the wood of pine trees in north temperate regions.

The specific name is derived from *argillosus* = full of clay.

Genus ***LUTAGO*** nov.

DIAGNOSIS. Anterior coxae globular and contiguous; middle coxae globular, separated by a distance equal to about one-quarter of the width of one coxa. Posterior coxae transverse, ratio width/length *c.* 2·0 : 1; the distance between the posterior coxae slightly less than the width of one coxa. First and second abdominal ventrites very large, their middle length together equal to four times the length of the third and fourth segments together. Prothorax transverse, without ocular lobes; the eyes half covered by the thorax when the head is deflexed. Scutellum small, triangular. Hindwings present.

TYPE SPECIES. *Lutago fetosus* sp. nov.

REMARKS. From the disposition of the coxae and the proportions of the abdominal ventrites the genus appears to be related to *Pissodites* (Pl. 4, fig. 2). It differs in that the hindbody and elytra are more transverse (ratio length/width of hindbody in *Pissodites c.* 1·8 : 1, in *Lutago c.* 1·3 : 1).

The generic name is masculine and is derived from *lutus* = mud.

Lutago fetosus sp. nov.

(Pl. 5, figs. 1, 2)

Diagnosis. As for genus.

Type material. *Holotype:* In.49372. A specimen including the prothorax. *Paratypes:* Twenty-one specimens. In.49373–49383, including the hindbody only; In.49041–49044, In.49078–49082, In.49087.

Measurements. Length 2·2–2·6 mm.; maximum width 1·1–1·5 mm.

Description. Ventral surface fairly uniformly punctured. Posterior margins of the middle coxae delimited by a faint groove. Middle length of the first and second ventrites together about twice the middle length of ventrites 3, 4 and 5 together. Metasternum with a transverse groove above each coxa. Elytral striae impressed and regularly punctured, the sutural stria with about 22 punctures. Intervals between the striae sparsely and faintly punctured.

Remarks. The specific name is derived from *fetosus* = prolific.

Other specimens. In.49088–49093. Length varying from 2·5–3·15 mm. Specimens include hindbody with or without elytra. Closely allied to *Lutago fetosus* sp. nov.

Lutago nanus sp. nov.

(Pl. 5, figs. 3, 4)

Diagnosis. The species is distinguishable from *L. fetosus* by its small size and coarse puncturation.

Type material. *Holotype:* In.49094. Including head, thorax, hindbody and elytra. *Paratypes:* Eight specimens. In.49095–49100, including hindbody with or without elytra; In.49389, including head, with broken rostrum, prothorax, hindbody and elytra; In.49390, including hindbody only.

Measurements. *Holotype:* length (including head and prothorax) 2·35 mm.; width 1·1 mm.; *Paratypes:* length (hind body and elytra only) 1·5–1·7 mm.; width 1·05–1·15 mm.

Description. Puncturation of the prothorax, and the ventral surface of the hindbody coarse, the punctures deep, fairly regularly spaced and separated by about their own diameter; the punctures of the remaining abdominal ventrites fine. Prothorax narrowed anteriorly, widest (*c.* 0·85 mm.) near the posterior angles, length 0·5 mm.; base of prothorax sinuate with a broad rounded projection in the middle. Elytral striae very coarsely punctured in the basal half, the punctures becoming smaller in the apical half. Sutural stria with about 18 punctures. Intervals between striae finely and sparsely punctured.

Remarks. The specific name is derived from *nanus* = dwarf.

Subfamily ERIRRHININAE Schönherr, 1826

Genus ***ERIRRHINITES*** nov.

DIAGNOSIS. Anterior coxae globular, almost contiguous. Prothorax without ocular lobes or anteroventral emargination. From the outer edge of each anterior coxal cavity arises a short, deep, curved groove, which extends about half-way to the anterior edge of the thorax. Rostrum slender, the ends of the scrobes visible as shallow depressions at the base. Metasternum strongly transverse, ratio width/middle length *c.* 3·0 : 1. Middle coxae globular, separated by about one-third of the width of one coxa. Posterior coxae transverse, elliptical, separated by about the width of one coxa. Posterior edge of the metasternum between coxae very obtusely angulate. Metasternum with a transverse groove above each posterior coxa, each groove ending in a pit at the inner end. Abdominal ventrites 1 and 2 very long, the suture between the two faint. Ratio of middle length of ventrite 1/ventrite 2/ ventrites 3–5 = 3·5 : 3·0 : 3·5.

TYPE SPECIES. *Erirrhinites bognorensis* sp. nov.

REMARKS. The generic name is masculine and is derived from *Erirrhinus*, a modern genus of weevils.

Erirrhinites bognorensis sp. nov.

(Pl. 6, figs. 1, 2)

DIAGNOSIS. As for genus.

TYPE MATERIAL. *Holotype:* In.49045.

MEASUREMENTS. Length (including head but not the rostrum) 3·5 mm.: maximum width 1·65 mm.; length of pronotum 1·15 mm.; length of elytra 2·45 mm.

DESCRIPTION. The prothorax is constricted anteriorly, being widest about one-third of its length from the base. The prothorax is densely punctured, the punctures on the dorsal surface being fainter than those on the anterior margin and ventral surface. This may be due to abrasion. The pronotum is without defined lateral margins. Elytral striae strongly and regularly punctured, the circular punctures separated by about their own length ; the third stria with 26 punctures. Intervals between striae slightly convex, sparsely and faintly punctured. Metasternum coarsely punctured. Ventrites fairly regularly punctured, the punctures much finer and more widely spaced than those on the ventral surface of the prothorax.

REMARKS. The species of the living genus *Erirrhinus* are found in marshy places, associated with reeds and sphagnum moss.

Erirrhinites sp. indet.

Specimen In.49422. Head and prothorax only. Head finely and densely punctured. Rostrum broken off close to the base. Eyes partly concealed by the prothorax. Maximum width of the prothorax 2·25 mm., middle length 1·75 mm. Anterior coxae globular (0·65 mm. wide) almost contiguous, finely punctured. Prothorax with slight ocular lobes and without defined lateral margins ; surface finely punctured on the anterior dorsal margin, elsewhere coarsely punctured and tuberculate and with a slightly raised median longitudinal line. From the outer edge of each anterior coxal cavity arises a short curved groove.

Subfamily CRYPTORRHYNCHINAE Schönherr, 1826

Tribe SOPHRONININI Lacordaire, 1866

Genus ***TAYLORIUS*** nov.

DIAGNOSIS. Rostrum moderately slender, cylindrical, slightly curved, apex reaching to a point between the middle coxae ; the ventral surface of the prothorax with a deep median channel for the reception of the rostrum, the channel continued on the mesosternum as far as the anterior edge of the metasternum, and enclosed at the sides between the anterior and middle coxae by a vertical flange ; prothorax with ocular lobes ; anterior coxae separated from each other by about 0·6 of their own width ; middle coxae separated by about their own width ; anterior edge of the metasternum between the middle coxae raised to form a transverse keel ; metasternum transverse, ratio width/length *c.* 2·0 : 1 ; junction between the metasternum and first ventrite marked by a curved suture, convex anteriorly, without trace of a median groove ; metasternum with a declivity anterior each posterior coxa ; first and second abdominal ventrites very large, their middle length twice as great as that of ventrites 3, 4 and 5 together. Elytra elongate, smooth, without tubercles.

TYPE SPECIES. *Taylorius litoralis* sp. nov.

REMARKS. The genus is named in honour of Mr. H. E. Taylor to whom we owe the discovery of the specimens on which this genus is based.

The gender of the generic name is masculine.

Taylorius litoralis sp. nov.

(Pl. 6, figs. 3, 4)

DIAGNOSIS. As for genus.

TYPE MATERIAL. *Holotype :* In.49340. A specimen which lacks only the legs, partly crushed dorsoventrally, length 4·4 mm. *Paratypes :* Seventeen specimens. In.49341, specimen which lacks only the legs ; elytra slightly crushed. In.49342–49352, comprising meso- and metathorax, abdomen and elytra, length 1·8–2·7 mm. In.49056–49059, consisting of meso- and metathorax, abdomen and elytra, length 2·5–3·0 mm. In.49060, a prothorax and head, with broken rostrum, showing the rostral groove very clearly.

MEASUREMENTS. *Holotype :* length head (pronotum and abdomen) 4·4 mm.; length of elytra 3·0 mm.; width of elytra 1·9 mm.

DESCRIPTION. Rostrum finely punctured ; head densely punctured, the punctures separated by less than their own width ; thorax densely and uniformly punctured, the average size of the punctures being twice that of the punctures on the head ; metasternum and ventrites coarsely and densely punctured ; punctures on the ventral surface separated by less than their own diameter ; density of punctures on the ventrites *c.* 450 per sq. mm.; pronotum without trace of a median line ; elytra rather parallel-sided, shoulders obvious, uniformly striate, each stria formed by a single row of large circular punctures which decrease in size slightly and uniformly but obviously from base to apex ; the punctures separated by less than their own diameter ; the third stria with about 33 punctures ; intervals between the striae flat and finely punctured.

REMARKS. The form of the rostral channel on the ventral side of the thorax allows *Taylorius* to be classified with a high degree of certainty. It must be placed in the Cryptorrhynchinae. The fact that the apical part of the rostrum is enclosed at the sides by vertical flange-like processes of the pro- and mesosterna, and that the apex of the rostrum rests in an indentation of the metasternum places the genus close to *Mecistocerus* in the Sophroninini. The modern *Mecistocerus* includes more than 150 species and is widely distributed throughout the tropics.

The specific name is derived from *litoralis* = of the shore.

Genus ***KORYSTINA*** nov.

DIAGNOSIS. Pronotum with the middle of the anterior edge produced into a short dorsoventrally flattened process which projects over the top of the head and is curved slightly downwards. Pronotum with ocular lobes present and the median longitudinal ventral channel deep and well defined. The channel ends in a cavity on the mesosternum into which the apex of the rostrum is fitted.

TYPE SPECIES. *Korystina gracilis* sp. nov.

REMARKS. The blunt process projecting forwards from the middle of the anterior edge of the pronotum is a very rare character in the Curculionidae. In the Cryptorrhynchinae it is found only in the modern species *Glyptoporopterus sharpi* Lea. A comparison of other characters, however, indicates that the pronotal process in *Glyptoporopterus* has been developed independently from that in *Korystina.* The termination of the thoracic channel on the mesosternum places *Korystina* with *Taylorius* in the Sophroninini.

The gender of the generic name is feminine, and the name is derived from *korystos* = helmeted.

Korystina gracilis sp. nov.

(Pl. 7, figs. 3, 4)

DIAGNOSIS. As for genus.

TYPE MATERIAL. *Holotype :* In.49692. A specimen including head, pronotum with rostrum lying in the prosternal channel, prothorax and the greater part of abdomen and elytra. *Paratype :* In.49693. Specimen comprising prothorax only.

MEASUREMENTS. Length of pronotum 1·8 mm. (holotype), 2·2 mm. (paratype). Maximum width of pronotum (at the base) 1·3 mm. (holotype), 2·0 mm. (paratype). Length of elytra (holotype) *c.* 3·2 mm.; width of elytra 1·5 mm.

DESCRIPTION. Pronotum with sides rounded anteriorly, widened at about the middle, then parallel-sided to the base ; without defined lateral margins, surface densely and evenly punctured; median anterior process of the pronotum broad, about one-fifth of the width of the base of the pronotum, slightly bilobed at the anterior end and with a median depression on the upper surface which is continued on to the pronotum; the depression is elliptical in shape and ends about one-third of the length of the pronotum from the apex of the process, which are separated from adjacent punctures in the stria by about one-quarter of the length of a puncture.

REMARKS. The specific name is derived from *gracilis* = slender.

Tribe CAMPTORRHININI Lacordaire, 1866

Genus ***CAMPTORRHINITES*** nov.

DIAGNOSIS. Prosternum with a deep median longitudinal channel for the reception of the rostrum; the channel opens anteriorly between the ocular lobes of the prothorax, passes back between the anterior coxae and is closed posteriorly just behind the coxae, before reaching the mesosternum. Anterior and middle coxae globular, the middle coxae separated by about half the width of one coxa. Posterior coxae transversely elliptical, ratio width/length *c.* 2 : 1, separated by about the length of a posterior coxa. Posterior edge of the metasternum between the coxae concave and obtusely angulate. Metasternum with a straight transverse declivity just anterior to the coxal cavity on each side. Rostrum slightly curved, stout, width about one-third of the length, with slight median and lateral longitudinal ridges; eyes elliptical, elongate in the dorsoventral direction, partly hidden by the rounded anterolateral lobes of the pronotum. The first and second abdominal ventrites very long; ratio of middle lengths of first and second ventrites together, the third and fourth ventrites together and the fifth ventrite alone *c.* 40 ; 7 ; 11. Elytra without tubercles, strongly punctate-striate. Pronotum simple, without protuberances.

TYPE SPECIES. *Camptorrhinites orarius* sp. nov.

REMARKS. The presence of a ventral median longitudinal channel for the reception of the rostrum places the genus in the subfamily Cryptorrhynchinae, while the fact that the channel ends on the prosternum and is closed at the posterior end limits the genus to the tribe Camptorrhinini. This is a small tribe, represented at the present time by one large genus, *Camptorrhinus*, and about four small genera. *Camptorrhinites* approaches most closely to the genus *Pachyonyx*, the species of which are African and Oriental. It differs from *Pachyonyx* in having the prothorax and elytra simple, not ornamented with protuberances.

The gender of generic name is masculine, and is derived from *Camptorrhinus*, a modern genus of weevils.

Camptorrhinites orarius sp. nov.

(Pl. 7, figs. 1, 2)

DIAGNOSIS. As for genus.

TYPE MATERIAL. *Holotype:* In.49353. A specimen including the head, thorax, abdomen and elytra; rostrum not entirely visible due to the lateral compression of the thorax. *Paratype:* In.49354. A specimen including the head, thorax, abdomen and elytra ; rostrum fully visible, but puncturation of the body largely obscured.

MEASUREMENTS. Length *c.* 5·0 mm. Length of elytra *c.* 3·5 mm.; width of elytra *c.* 2·5 mm. Length of rostrum 0·7 mm. Length of pronotum *c.* 1·7 mm.; depth *c.* 2·0 mm.

DESCRIPTION. Head and pronotum densely and uniformly punctured, with punctures on the pronotum about twice as large as those on the head and separated by less than their own diameter ; punctures on the sides of the thorax two or three times as large as those on the dorsal surface ; all coxae, the metasternum and abdomen coarsely punctured like the sides of the prothorax except on the apical ventrite where the punctures are finer ; elytra uniformly striate, each stria formed by a row of large circular punctures separated from each other by less than their own length. Stria 4 with 22 punctures. Intervals between the striae slightly convex and finely but sparsely punctured.

REMARKS. The specific name is derived from *orarius* = of the coast.

Camptorrhinites spp. indet.

One specimen (In.49425) comprising the prothorax only. Length 2·25 mm.; depth (dorsoventral) 2·0 mm.; maximum width 2·1 mm. Prothorax closely and uniformly punctured, with a trace of a dorsal median longitudinal ridge ; with ocular lobes ; anterior coxae globular. The prosternal channel is obvious, opening anteriorly, but apparently not reaching the posterior edge of the prosternum. This would place the genus near *Camptorrhinites*. It differs from *C. orarius* by its larger size and the trace of a median longitudinal ridge.

One specimen (In.49426) hindbody and left elytron only. Length 1·85 mm.; maximum width 1·0 mm. Middle coxae globular with a cavity as wide as one coxa between them, the cavity closed behind by a transverse ridge. Posterior coxae transverse ovoid (0·18 × 0·30 mm.) separated by about 0·2 mm. Metasternum strongly transverse, without trace of a median impressed line ; posterior edge between the coxae slightly curved, not angulate in the middle ; coarsely and deeply punctured, the punctures separated by about their own width. First and second ventrites of the abdomen very large and apparently fused, length of the two ventrites together 0·85 mm., maximum width (at base) 0·85 mm. Length of the last three ventrites together 0·4 mm. Whole surface of the ventrites uniformly punctured like the metasternum. Elytral striae each marked by a longitudinal row of circular punctures separated by their own width.

CURCULIONIDAE gen. et spp. indet.

In.49355–49358. Comprising meso- and metathorax, abdomen and elytra. Length, 3·0–3·5 mm.; maximum width (at shoulders of elytra) *c.* 2·0 mm. Middle coxae globular, finely punctured, separated by median processes of meso- and metathorax which meet between the coxae ; the coxae separated by about one-fifth of the width of one coxa. Width of metasternum *c.* 1·65 mm., middle length of metasternum

0·6 mm. Sides of the metasternum very coarsely punctured, the surface having a reticulate appearance ; lower margins of the middle coxae delimited by a row of very coarse punctures ; middle and posterior parts of the metasternum closely, but more finely punctured than the sides ; posterior edge of the metasternum between the posterior coxae obtusely angulate with a very short median groove at the angle ; first and second ventrites very large, about twice as long as the last three ventrites together ; basal (first) ventrite punctured like the metasternum ; posterior coxae elliptical, separated by a distance equal to the width of one coxa. Elytral striae marked by very deep, elongate punctures, separated at most by their own length ; sutural stria with about 24 punctures ; intervals between striae moderately convex, very finely but sparsely punctured.

In.49068–49071. Comprising hindbody and elytra only. Length 4·6–5·5 mm., maximum width 3·5–4·0 mm. Closely related to the above four specimens in form and puncturation, but of much larger size.

In.49359. Length 6·2 mm., maximum width (across base of elytra) 3·1 mm.; length of elytra 4·4 mm. A specimen including head, prothorax and hindbody with elytra. The rostrum is missing, broken off close to the head. Eyes dorsoventrally elongate. Anterior coxae approximately globular, contiguous. Middle coxae globular, separated by about one-fifth of the width of one coxa. Metasternum width 2·65 mm., middle length 1·0 mm. Posterior edge of the metasternum between the coxae obtusely angulate, the coxae separated by 0·75 of the width of a coxa. Metasternum with a very short median groove extending forwards from the obtuse angle of the posterior edge. Ratio of middle length of first ventrite : second ventrite : third to fifth ventrites together, 2 : 1 : 2·5. Puncturation on the ventral surface is largely obliterated except on the first and second ventrites which have traces of dense puncturation. Elytral striae impressed and regularly punctured, sutural stria with about 26 punctures. Intervals between stria moderately convex, each with a row of very sparse fine punctures.

In.49366–49369. Comprising hindbody and elytra only. Length *c.* 4·0 mm., width 2·5 mm. Middle coxae globular, separated by about one-third of the width of one coxa. Posterior edge of the metasternum obtusely angulate, with a short median groove extending forward from the angle. Posterior coxae separated by about 0·75 of the width of one coxa. Length of first and second ventrites/length of third, fourth and fifth ventrites, *c.* 3/2. Ventral surface densely and fairly uniformly punctured. Elytral striae marked by large, deep, regularly spaced punctures, which are separated by about their own length. Towards the apex the striae are impressed and the punctures become smaller. Sutural interval with *c.* 29 punctures.

In.49360–49363, In.49061–49065. Comprising hindbody and elytra only. Length, 4·0–5·5 mm., width 2·0–3·25 mm. Middle coxae globular, separated by about half the width of one coxa. Posterior coxae separated by about the width of one coxa. Posterior edge of the metasternum curved, without a median groove. Ratio of length of first ventrite/second ventrite/third to fifth ventrites together, 4/3/3. Ventral surface densely and fairly uniformly punctured.

In.49364–49365, In.49072. Comprising hindbody and elytra only. Length, 2·75–3·5 mm. Middle coxae globular, separated by about one-fifth of the width of one coxa. Metasternum width/middle length *c.* 2·5 mm., surface moderately convex on each side of the middle. Posterior coxae separated by about half the width of one coxa. Metasternum with a transverse fold above each posterior coxa. Fifth ventrite almost as long as the first or the second ventrites. Third and fourth ventrites short. Ventral surface densely and fairly uniformly punctured. Elytral striae impressed and punctured, the punctures becoming smaller and the striae deeper towards the apex.

In.49370–49371, In.49073, In.43369–43370. Maximum width 2·5–2·75 mm. Middle coxae globular, separated from each other by about one-quarter of the width of one coxa. Posterior coxae separated by about two-thirds of the width of a coxa. Posterior margin of the middle coxae and posterior coxae defined by a punctured groove. Metasternum with a transverse groove above each posterior coxa, ending in a deep pit at the inner end. Fifth ventrite, second and first ventrite at the side behind the coxa about equal in length. Third and fourth ventrites very short, their length together less than that of the fifth ventrite. Whole ventral surface densely and finely punctured, the punctures of the first ventrite between the coxae a little coarser than elsewhere. Elytra with striae finely punctured (about 20 punctures) in the basal half, the punctures becoming obliterated and the striae impressed in the apical half. Intervals between the striae flat except at the apex. Intervals finely and sparsely punctured.

In.49074–49077. Fragments of hindbody and elytra. Recognizable as Curculionidae by the posterior coxae and proportions of the lengths of the ventrites.

In.49697. Apical third of the elytra and the last three ventrites of the abdomen.

In.49698. Head (lacking the rostrum) and prothorax. Length 1·0 mm., maximum width, at the base of the prothorax, 0·95 mm.

In.49699. Abdomen and part of the metasternum. Length 1·95 mm.

In.49700. Head (with greater part of rostrum lacking) and anterior half of the pronotum. Length 2·5 mm., width 2·8 mm.

In.49701. Head (with greater part of the rostrum lacking) and prothorax, with anterior coxae. Length 1·85 mm., maximum width, near middle of the thorax, 1·95 mm. Coxae globular and contiguous. Lateral edges of pronotum uniformly curved, anterior and posterior angles broadly rounded.

In.49702. Meso- and metathorax and abdomen, and inner impressions of the elytra. Length 4·75 mm., maximum width of the metasternum 1·5 mm. Middle coxae circular, almost contiguous. Metasternum coarsely and rather sparsely punctured, and with a short deep median groove running forwards from the middle of the base. Posterior coxae transverse elliptical, faintly punctured. First and second ventrites each about twice as long as the third and fourth respectively.

In.49703. Base of left elytron with left middle and posterior coxae and part of metasternum.

In.49388. Hindbody without elytra.

In.49046–49055, In.49086. Hindbody with or without elytra.

In.49391–49392. Hindbody and elytra only. Length 4·5–4·75 mm., width 3·0–3·5 mm. Sutural striae with 25 punctures. Middle coxal cavities each with a raised posterior rim, outlined by a curved row of very coarse, coalescent punctures which form a deep groove. First abdominal ventrite with a row of very coarse semi-coalescent punctures which outlines a raised basal margin. Metasternum very coarsely punctured at the sides.

In.49424. Fragment of a right elytron. Length 5 mm.

In.49419. Hindbody and elytra. Length 3·6 mm.

In.49420. Hindbody and elytra, and part of posterior right femur. Elytra and ventral surface very deeply and coarsely punctured.

In.49421. Hindbody only. Length 3·4 mm. Puncturation of ventral surface largely obliterated, visible only on sides of metasternum and abdomen. Middle coxae globular, separated by about one coxa width ; posterior coxae transverse ovoid, separated by about one coxa length ; segmentation of abdomen obscured.

In.49422. Head (with rostrum lacking) and prothorax. Coxae globular and contiguous ; dorsal and ventral surfaces coarsely granulate. Pronotum without defined lateral margins, so that there is no boundary between dorsal and ventral surfaces. Pronotum length 1·6 mm., maximum width (near base) 2·4 mm. The size, shape and the contiguous front coxae suggest that this specimen may belong to the same species as In.48355.

In.49083–49085, In.49384–49387. Including the hindbody, with or without elytra. Length 2·0–2·25 mm., width 1·25–1·5 mm. This species is recognizable by the dense uniform puncturation of the ventral surface, the broad depression covering the middle of the posterior half of the metasternum, the middle third of the first ventrite and the anterior part of the second ventrite, and lastly by the extremely short third and fourth ventrites. Proportions of the middle length of the first to fifth ventrites are 26/24/5/5/11. Middle coxae globular, separated by about one-quarter of the width of the width of one coxa. Posterior coxae separated by the width of one coxa. Elytral striae marked by large deep, regularly spaced punctures. Intervals between the striae very finely punctured. The sutural striae with about 24 punctures.

In.49033–49034. Hindbody only. Length 2·25 mm., width 1·1–1·3 mm. Middle coxae globular, contiguous. Metasternum inflated with a groove around the posterior margin of the coxae and a very short median longitudinal groove arising from the posterior edge. Abdominal ventrites 1 and 2 long, 3 and 4 very short.

In.49035. A femur and base of a tibia of a weevil. Length 2·0 mm., maximum width 9·75 mm., with a prominent tooth on the under side.

In.49036–49040. In.37734–37735. These specimens are the hindbodies of several species of weevils. They are in poor condition and cannot be identified with certainty with any other specimen.

In.49334–49337. Including hindbody and elytra. Length 2·5–3·0 mm., width 1·4–1·9 mm. Resembles *Lutago fetosus* in the puncturation of the ventral surface and in the punctured groove to the posterior edges of the middle coxae. It differs by being larger and by the transverse groove above each posterior coxa. This groove ends on the inner side in a deep pit. Elytral striae coarsely but regularly punctured, the punctures separated by about their own length. Sutural stria with about 20 punctures. Intervals between striae moderately convex, rather sparsely and faintly punctured.

In.49338–49339. One specimen including metathorax and abdomen with punctuation obliterated. The second specimen comprising the abdomen only, densely punctured.

In.49066–49067. Hindbody and elytra only. Length 3·75 mm., width 2·5 mm. Metasternum and ventrites densely and fairly uniformly punctured, the punctures separated by less than their own diameter. Middle coxae globular, separated by about half the diameter of one coxa. Posterior coxa separated by about the width of one coxa. First and second ventrites very large and the third and fourth very short. Ratio of middle lengths of ventrites 1, 2, 3, 4, 5, is 23/20/3/3/8. Suture between ventrites 1 and 2 rather faint. Elytral striae strongly punctured, the punctures circular and separated by less than their own diameter. Intervals between striae finely punctured.

In.49417–49418. Hindbody only. Length 2·1 and 1·6 mm. Width, 1·5 and 1·1 mm. Puncturation obscured.

CARABIDAE gen. et spp. indet.

In.49433. Comprising the head of a carabid beetle. Length from the middle of the anterior edge of the clypeus 1·8 mm., width across the eyes 2·0 mm. Of the mandibles only the base of the left and the basal half of the right are present. Labrum missing, clypeus clearly visible, quadrate, transverse. Front with a longitudinal groove immediately above each eye. Eyes strongly convex. On the ventral surface the typical bilobed mentum is visible together with the basal segment of the left labial palp. Submentum with a strong transverse depression.

The specimen appears to belong to the Pterostichini, a tribe which includes many species of carnivorous ground beetles.

In.37736. Basal portion of a large elytron, length 5·5 mm., width (complete) 2·5 mm. Striae strongly and regularly punctured, the circular punctures separated by about their own length ; intervals between striae flat ; a long scutellar striole bearing 14 punctures is present at the base on the inner side.

COLEOPTERA indet.

By reason of their incompleteness the following specimens of Coleoptera cannot be referred to a family with certainty.

In.49423. Length 2 mm., including only the abdomen and posterior half of the elytra of a beetle. First and second ventrites each about twice as long as each of the third and fourth ventrites. Fifth (terminal) ventrite very large, as long as the first and second ventrites together. This ventrite is rounded apically and has a broad ventral depression beginning near the middle of the ventrite and widening to the apex. All ventrites fairly densely punctured. Elytra deeply striate, each stria about half as wide as the adjoining intervals and faintly punctured. Intervals between striae moderately convex, with fine punctures of two sizes, the larger punctures arranged in a line more or less in the middle of the interval ; smaller punctures of about half the diameter of the larger punctures more numerous and scattered.

In.49435. Comprising the greater part of the right elytron of a beetle. Length 6·5 mm., maximum width 3·5 mm. Only the basal quarter of the elytron is not obscured. This shows nine impressed and punctured longitudinal striae. There is no scutellar striole, and the intervals between striae are convex and finely and sparsely punctured. More precise identification is not possible but the appearance of the elytron suggests that the species might belong to the Curculionidae.

In.49436. Comprising the abdomen of an insect. Length 3·75 mm., maximum width 2·5 mm., with six visible segments. It is not possible to assign it with certainty to the Coleoptera.

In.49437. Including the abdomen and left elytron of a beetle. Length 3·25 mm., maximum width 2·5 mm. The abdomen is obscured with the exception of the terminal ventrite which is unpunctured. A small triangular scutellum is visible at the base of the inner edge of the elytron. Elytron with seven visible striae, which are longitudinal, equally spaced, faintly and regularly punctured. Intervals between striae flat, unpunctured. Shoulder of the elytron prominent, square.

In.40438. Abdomen of a beetle with posterior and middle coxae attached. Length 4·6 mm., maximum width 3·75 mm. The metasternum is reduced or crushed so that the middle and posterior coxae are in contact. Five ventrites are marked by irregular grooves which are mainly longitudinal in the middle. In addition the surface of the ventrites is fairly closely punctured. Width of the basal ventrite 3·75 mm. The abdomen is tapered to the apex, the width of the apical ventrite being 2·1 mm.

In.49439. Consisting of the elytra of a beetle. Length 4·6 mm., maximum width 2·6 mm. Longitudinal striae impressed and faintly punctured. Intervals between striae slightly convex and sparsely punctured. Elytra with shoulders obvious, parallel sided to about the middle then tapered to the apex.

In.43365–43368. Fragments of four species of Coleoptera.

Specimens other than Coleoptera

Order HEMIPTERA

Suborder HETEROPTERA

Family Pentatomidae Leach, 1815

Subfamily Pentatominae Leach, 1815

Genera and species indeterminate

In.49442. Including head and prothorax with anterior coxae. Length, 3·0 mm., width across prothorax 3·0 mm.

In.49443. Including head, part of the thorax, with all three pairs of coxae and the scutellum. In this specimen and In.49442 the bucculae are visible on the underside of the head, and on the dorsal side the sutures dividing off the tylus from the jugae.

In.49444. Including part of the abdomen only. Length 2·85 mm., width 2·5 mm.

IV. ACKNOWLEDGMENTS

I wish to record my thanks to the following: Mr. H. E. Taylor and Mr. E. M. Venables for information on their methods of collecting; Dr. E. I. White, F.R.S., Keeper of Palaeontology, British Museum (Natural History) for permission to study the material; Dr. H. W. Ball and Mr. R. Baker of the Department of Palaeontology for assistance in the preparation of the manuscript; Mr. J. Brown, Photographic Section, for skilful photography, and to my colleagues in the Department of Entomology for useful discussion of the material.

PLATE 2

FIG. 1. *Venablesia colluvium* gen. et sp. nov. Ventral. Holotype, In.49102, × 25.
FIG. 2. *Stagetus denticornis* Champion. (Recent.) Ventral, × 25.
FIG. 3. *Venablesia colluvium* gen. et sp. nov. Dorsal, holotype, × 25.
FIG. 4. *Pactopus avitus* sp. nov. Dorsal. Holotype, In.49404, × 15.

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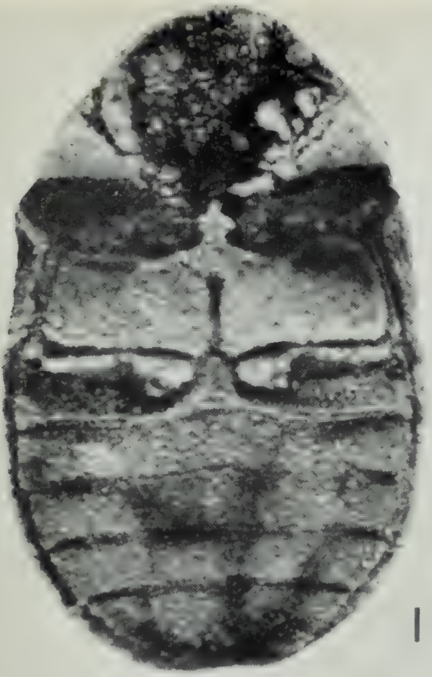

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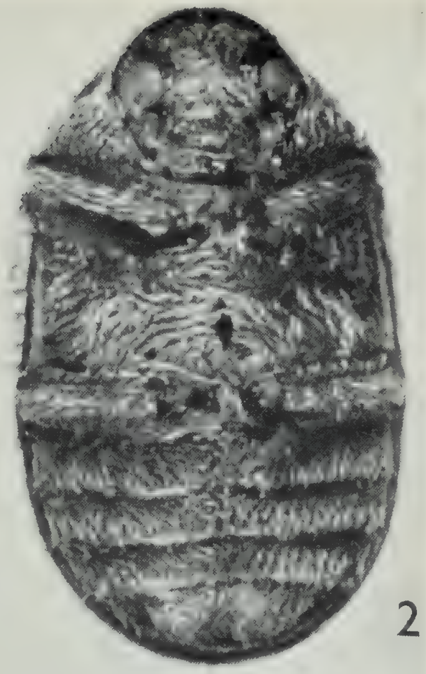

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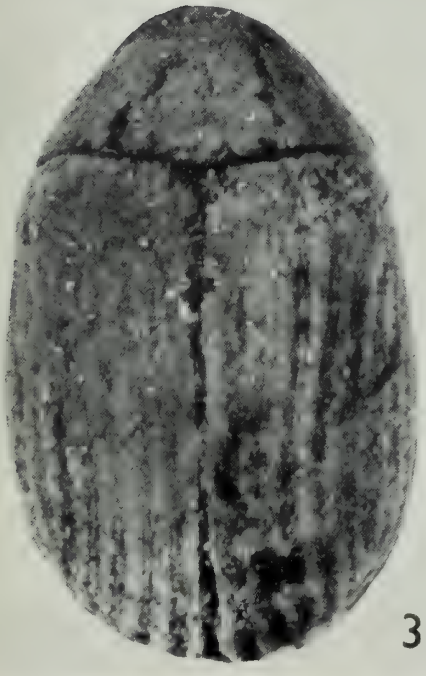

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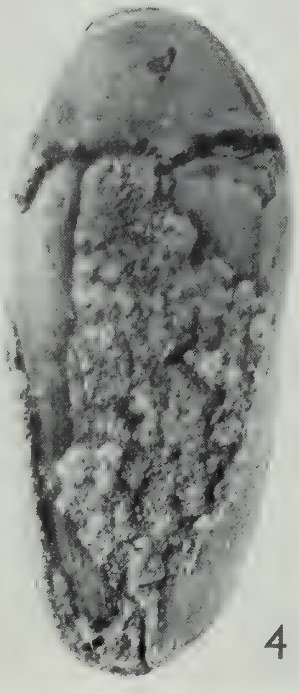

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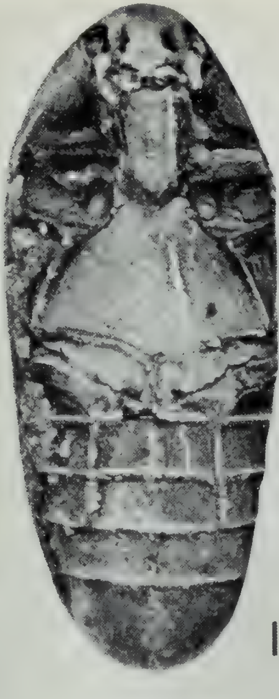
PLATE 3

FIG. 1. *Pactopus avitus* sp. nov. Ventral. Holotype, In.49404, × 25.
FIG. 2. *Pactopus horni* LeConte. (Recent.) Ventral, × 15.
FIG. 3. *Potergites senectus* gen. et sp. nov. Dorsal. Holotype, In.49405, × 28.
FIG. 4. *Potergites senectus* gen. et sp. nov. Same specimen, ventral, × 28.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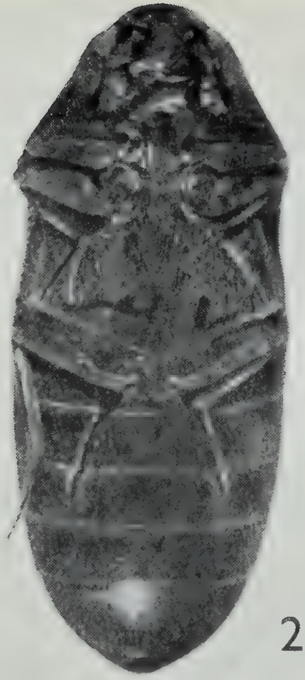
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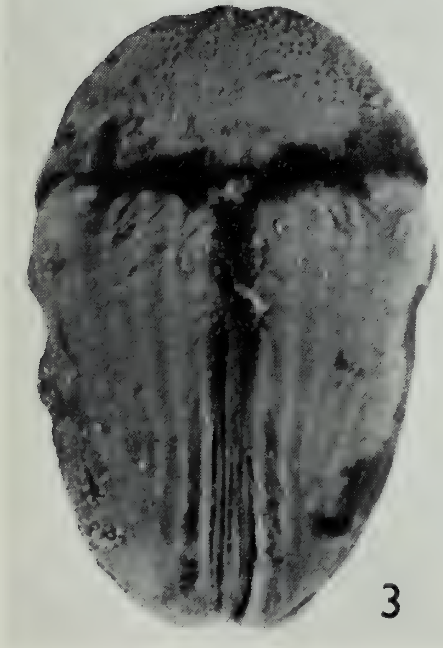
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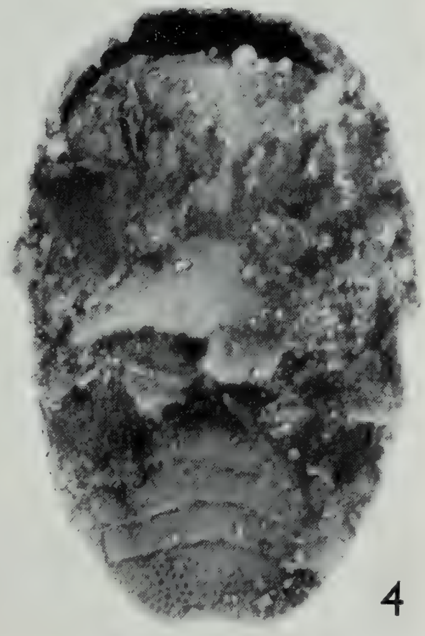
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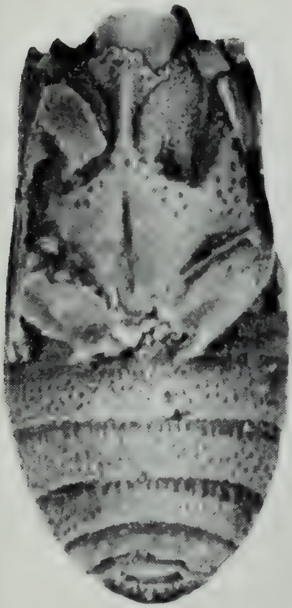
PLATE 4

FIG. 1. *Saprosites cascus* sp. nov. Ventral. Holotype, In.49695, × 30.
FIG. 2. *Pissodes castaneus* Degeer. (Recent.) Ventral, × 14.
FIG. 3. *Pissodites argillosus* gen. et sp. nov. Ventral. Holotype, In. 49325, × 30.
FIG. 4. *Pissodites argillosus* gen. et sp. nov. Same specimen, dorsal, × 30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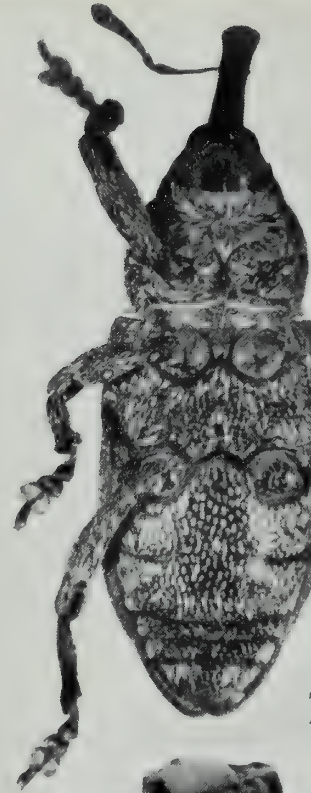
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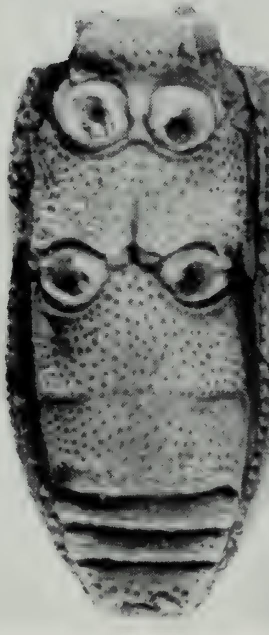
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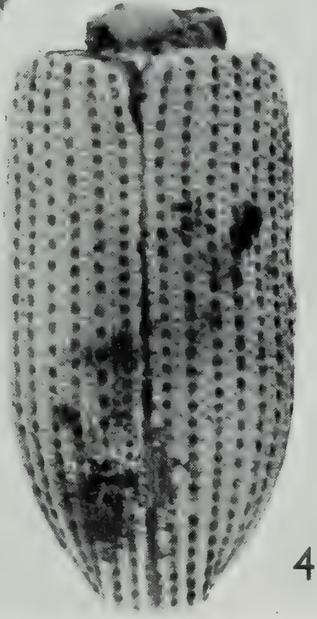
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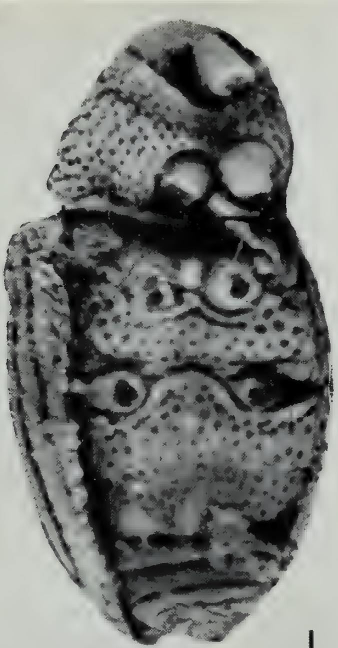
PLATE 5

Fig. 1. *Lutago fetosus* gen. et sp. nov. Ventral. Holotype, In.49372, × 33.
Fig. 2. *Lutago fetosus* gen. et sp. nov. Same specimen, dorsal, × 33.
Fig. 3. *Lutago nanus* gen. et sp. nov. Dorsal. Holotype, In.49094, × 38.
Fig. 4. *Lutago nanus* gen. et sp. nov. Same specimen, ventral, × 38.



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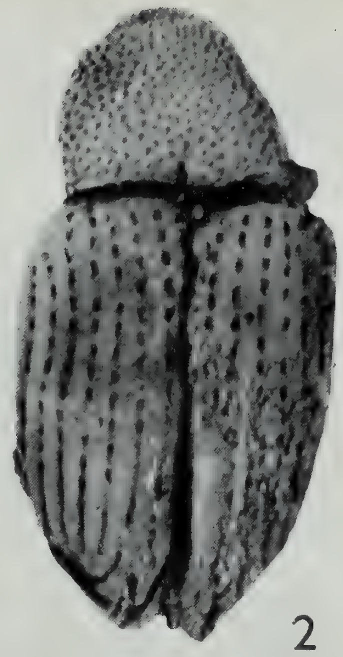

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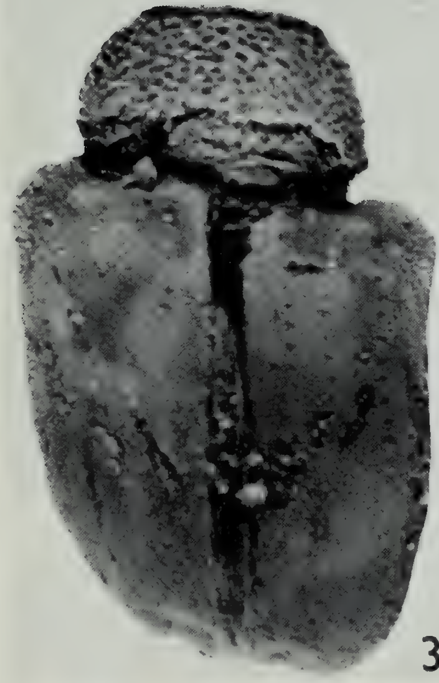

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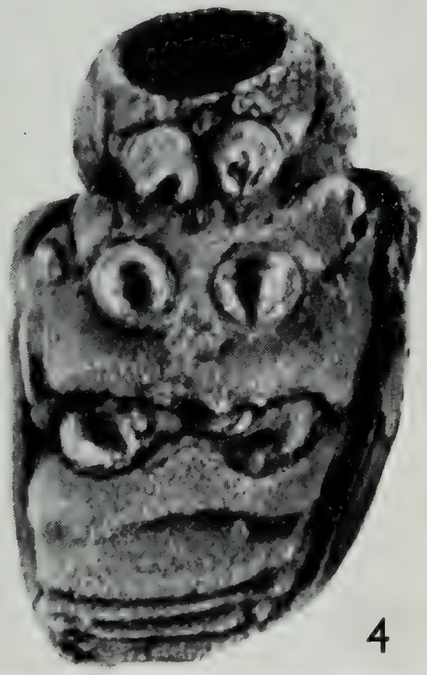

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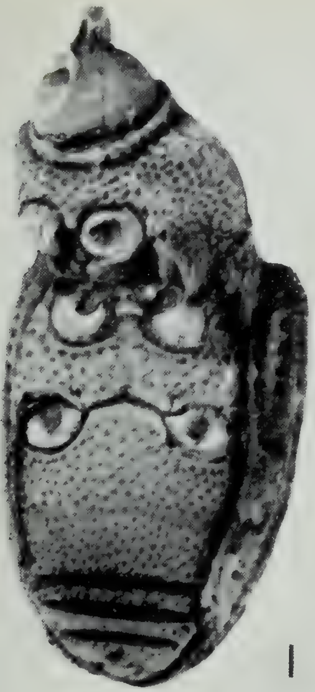
PLATE 6

FIG. 1. *Erirrhinites bognorensis* gen. et sp. nov. Ventral. Holotype, In.49045, × 26.
FIG. 2. *Erirrhinites bognorensis* gen. et sp. nov. Same specimen, dorsal, × 26.
FIG. 3. *Taylorius litoralis* gen. et sp. nov. Dorsal. Holotype, In.49340, × 20.
FIG. 4. *Taylorius litoralis* gen. et sp. nov. Same specimen, ventral, × 20.



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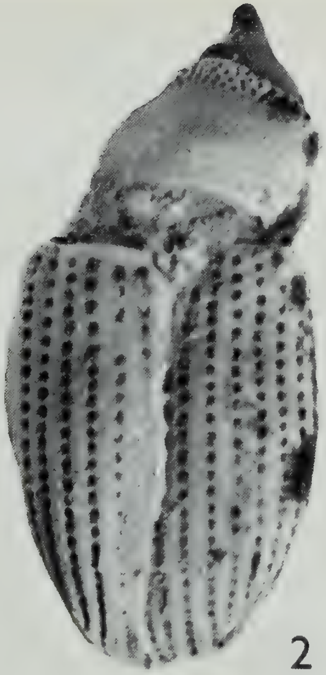

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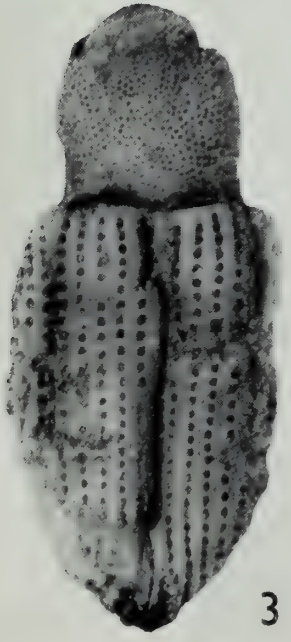

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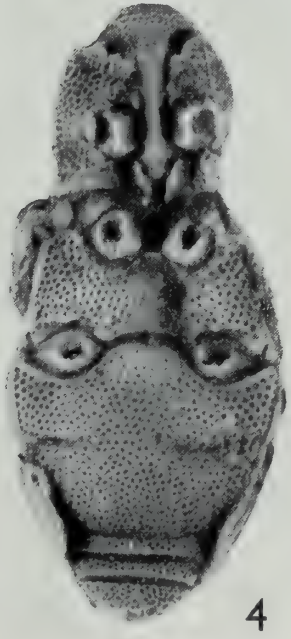

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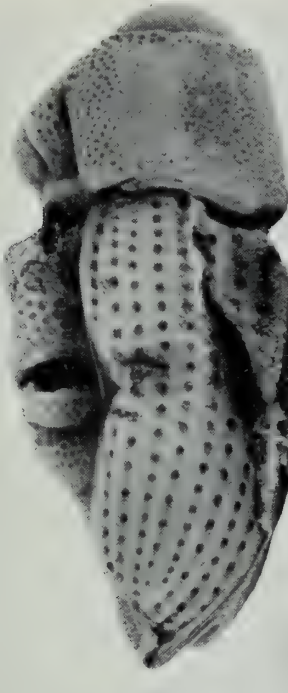
PLATE 7

FIG. 1. *Camptorrhinites orarius* gen. et sp. nov. Lateral. Holotype, In.49353, × 18.
FIG. 2. *Camptorrhinites orarius* gen. et sp. nov. Same specimen, ventral, × 18.
FIG. 3. *Korystina gracilis* gen. et sp. nov. Dorsal. Holotype, In.49692, × 18.
FIG. 4. *Korystina gracilis* gen. et sp. nov. Same specimen, ventral, × 18.



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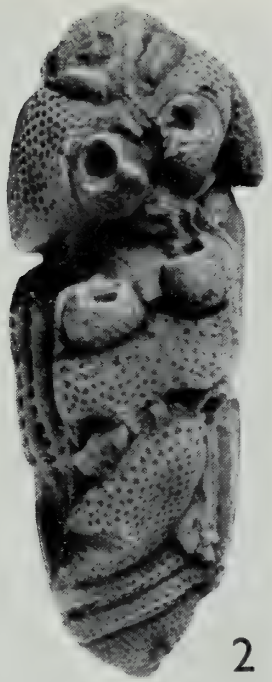

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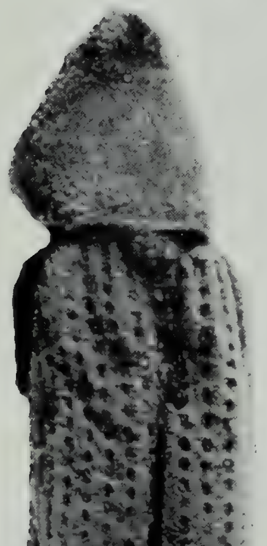

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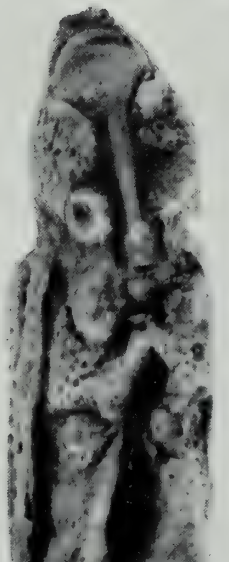

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THE MORPHOLOGY AND RELATIONSHIPS OF *RACHIOPTERIS CYLINDRICA*

BRITISH MUSEUM
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NATURAL HISTORY

H. S. HOLDEN

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
GEOLOGY Vol. 4 No. 3
LONDON : 1960

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Pp. 51–69 ; *Plates* 8–10 ; 6 *Text-figures*

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THE MORPHOLOGY AND RELATIONSHIPS OF *RACHIOPTERIS CYLINDRICA* WILLIAMSON

By HENRY SMITH HOLDEN

SYNOPSIS

The anatomy of *Psalixochlaena cylindrica* (Will.), a fern from the Coal Measures, originally described by Williamson as *Rachiopteris cylindrica,* is described and its affinities with other possibly related Palaeozoic ferns is discussed.

The anatomy of *Rhabdoxylon dichotomum* gen. et. sp. nov., also a Palaeozoic fern formerly interpreted as a marsh ecotype of *Rachiopteris cylindrica,* is described and its probable affinities indicated.

INTRODUCTION

THE earliest account of the morphology of the Coal Measure fern which forms the subject of this paper was that of Williamson (1878) who assigned it to his comprehensive genus *Rachiopteris* and created a new species *R. cylindrica* for its reception. His material which appears to have been inadequate for more than a brief description was obtained from a Halifax locality and he regarded its inclusion in the genus *Rachiopteris* as purely provisional. A more detailed account based on the sections in the Cash and other collections in the Manchester University Museum was published by Hick (1896). It is probable that the sections described by Hick were also from the Halifax district since those in the Cash Collection at least were prepared by James Binns who resided in that area. Hick, although inclined to the view that *R. cylindrica* was a fern, left the question of its affinities undecided. In the light of our further knowledge, however, it is now generally agreed that it should be assigned to the Filicales.

A more detailed study of the plant was made by the late Helen Bancroft (1915) who examined not only the specimens described by Hick and by Williamson but also the specimens which the late F. W. Oliver had purchased over a period of years for University College (London). In addition she studied the relevant slides in the Cambridge University Collections and those belonging to the late W. T. Gordon. All the material studied by her came from Yorkshire localities and she suggested that the plant may have been confined to the Yorkshire coalfield. There is no doubt, however, that it occurred elsewhere though less commonly since there are now records of its discovery in coal-balls from Burnley, Bacup and other localities on the Lancashire side of the Pennines. There is also a solitary section (Scott Coll. 2012) from Booth Hill Colliery, near Oldham. It is worthy of note that, apart from its occurrence in coal-balls from both Lancashire and Yorkshire, it has now been recorded and figured by Leclercq (1925) from Belgium and by Kraentzel (1934) from both Holland and Belgium.

Bancroft, on the basis of the specimens examined by her, included two types of stem which she designated as Types α and β in *Rachiopteris cylindrica* her Type α stem having a larger stele and a much more robust build than Type β which she interpreted as representing the semi-aquatic or marsh variety of the species. It should be pointed out, however, that Williamson only applied the name *Rachiopteris cylindrica* to the specimens grouped by Bancroft under her Type α although he referred to and figured a transverse section of a stem clearly belonging to her Type β (Williamson 1878, pl. 24, fig. 88) which he suggested might well be related to *R. cylindrica*.

The present account is based very largely on specimens in the Kidston and Scott Collections together with those in the collection of the author. In addition to these the slides in the Oliver Collection now, like those of the author, in the Department of Palaeontology, British Museum (Natural History), and those in the Williamson Collection have been re-examined as well as individual slides from other sources. The study of this relatively large number of specimens has led to a fuller knowledge of the plant and to a re-assessment of its systematic position and of its relationships to the other Palaeozoic ferns usually included in the Botryopterideae.

It is proposed to describe first the plant named *Rachiopteris cylindrica* by Williamson (i.e. Bancroft's Type α) and to describe and discuss the relationships of Bancroft's Type β later in this paper.

SYSTEMATIC DESCRIPTION

Genus ***PSALIXOCHLAENA*** nov.

DIAGNOSIS. A fern possessing a slender stem with the immature parts at least densely clothed with unbranched multicellular hairs ; stem stele cylindrical consisting entirely of tracheids differentiated into a central group of small tracheids enclosed by a peripheral system of larger ones. Protoxylem mesarch forming two to five groups lying at the junction of the large and small tracheidal members of the stele. Xylem surrounded by a continuous sheath of xylem parenchyma, phloem and phloem parenchyma. Cortex differentiated into parenchymatous inner zone, sclerized middle zone and narrow parenchymatous outer zone ; branching of the stem unequal the daughter stem always smaller then the parent stem and, in most cases, initially possessing two immersed protoxylem groups though occasionally possessing one only. Petioles arising from the stem singly at irregular intervals, circinately coiled when young with a monodesmic vascular supply consisting near its base of a flattened xylem cylinder with the protoxylem at first distributed discontinuously along its adaxial face but soon forming three well-defined ridges : developing a pronounced abaxial curvature distally and thus becoming C-shaped in transverse section. Pinna traces monarch, marginal, given off alternately from the right and left sides of the parent strand and bifurcating repeatedly. Roots uniformly diarch with well-defined endodermis and exodermis. Root hairs present and probably persistent.

TYPE SPECIES. *Psalixochlaena cylindrica* (Will.).

Psalixochlaena cylindrica (Williamson) nov. comb.

Pls. 8, 9; Pl. 10, figs. 1–4

1878 *Rachiopteris cylindrica* Williamson, p. 351, pl. 24, figs. 80–84, 86, 87.
1896 *Rachiopteris cylindrica* Will.: Hick, p. 1, pl. 1, fig. 5.
1908 "*Rachiopteris cylindrica*" Will.: Tansley, p. 14, text-fig. 14.
1908 *Rachiopteris cylindrica* Will.: Scott, p. 333.
1910 *Botryopteris cylindrica* (Will.) Seward, p. 438, text-figs. 305A, B.
1915 *Rachiopteris cylindrica* Will. (Type α): Bancroft, p. 532, pl. 26, figs. 1, 2, 6; pl. 27, figs. 1, 3, 4; text-figs. 1–7, 9, 10.
1920 *Botryopteris cylindrica* (Will.): Scott, p. 345, text-fig. 156.
1923 *Botryopteris cylindrica* (Will.): Bower, p. 121, text-fig. 114.
1925 *Botryopteris cylindrica* (Will.): Leclercq, p. 58, pl. 46, figs. 8, 9; pl. 47, fig. 10.
1926 *Botryopteris cylindrica* (Will.): Bower, p. 10, text-fig. 312.
1927 *Botryopteris cylindrica* (Will.)—Forma α—: Hirmer, p. 533, text-figs. 648, 649.
1940 *Botryopteris cylindrica* (Will.): Walton, p. 100, text-fig. 75.

DIAGNOSIS. As for genus.

HOLOTYPE. A transverse section of the stem figured by Williamson (1878, pl. 24, fig. 80). Williamson Colln. slide no. 179.

DESCRIPTION. *Stem*: The stem varies in diameter, in the specimens measured, from 2·0 to 2·3 mm. and that of the stelar xylem from 0·7 to 0·8 mm. The latter consists entirely of tracheids which form a cylindrical core to the stem except where their symmetry is modified by the emission of petiole or root traces or by branching (Pl. 8, fig. 2). In typical specimens the central part of the xylem cylinder is formed of relatively small tracheids surrounded by a zone of tracheids of larger diameter the protoxylem groups, varying in number from two to five, lying at the periphery of the smaller, centrally situated ones and hence being mesarch in position (Pl. 8, fig. 1). Variations from this type of structure are infrequent but very rarely specimens occur in which there is a single centrally situated group of protoxylem, that is, in which the protoxylem is centrarch (Bancroft, 1915, pl. 26, fig. 2).

A still more unusual departure from the typical stelar condition is illustrated by two transverse sections of a stem (Holden Colln. nos. 618, 619) which has been cut transversely at a level at which there are four outgoing root traces and where the stem is preparing to branch. As in typical specimens the xylem of the stem is differentiated into a central group of small tracheids surrounded by tracheids of larger calibre. It differs, however, in possessing an additional cylinder of small tracheids external to the larger ones (Pl. 9, fig. 8). The cells of the conjunctive parenchyma immediately external to these small tracheids have divided in a number of places to form flattened cambiform daughter cells. Whether this indicates that the system of small peripherally situated tracheids is of secondary origin is, however, a matter of some doubt since they show no indication of the regular radial arrangement typical of secondary xylem.

The pits, which are present on all faces of the tracheids, vary from the reticulate type with transversely elongated pits on the wider walls to the scalariform type on those which are narrower. There has been some doubt as to the nature of the thickening of the tracheids forming the protoxylem. Bancroft considered that this was scalariform and that the type of thickening was possibly to be correlated with relatively slow growth. The thin sections made possible by modern " peel " techniques have shown, however, that these possess spiral thickenings, a feature which they share with the petiolar protoxylem. The xylem is surrounded by a continuous zone of xylem parenchyma, phloem and phloem parenchyma the phloem consisting of a more or less continuous series of large sieve tubes enclosed on either side by the smaller and frequently somewhat tangentially flattened cells of the xylem and phloem parenchyma respectively. External to the phloem and its associated parenchyma there is usually a fairly well defined layer of cells with dark contents which may be interpreted as an endodermis (Pl. 8, fig. 2, Pl. 9, fig. 2). The cortex is divisible into three zones the innermost of which is parenchymatous. The middle cortex is composed of thick-walled cells and, together with the stelar xylem, is, in the less well preserved examples, the only tissue surviving petrifaction. Even when the stele and all the tissues up to and including the middle cortex are present it is very rare to find any trace of the outer cortex and surface tissues. The erosion of these tissues renders it difficult to determine what their normal character was during life though Bancroft has recorded and figured their local survival (Bancroft, 1915, text-fig. 4*a–c*). From her figures it seems probable that the epidermis bore multicellular hairs and this view is strengthened by the good fortune of the author in possessing an obliquely longitudinal section (Holden Colln. 611) passing through the apex of the stem and a series of transverse " peels " (301D 60–70) also passing through the apical region. Text-fig. 1 illustrates the general build of the obliquely longitudinal section which shows, at the lower end, an oblique section of the stem stele from which both a root and petiole trace are being given off. Some distance nearer the apex a root cut transversely is shown embedded in the tissues of the cortex. The apex itself clearly has the form of a blunt dome-shaped mass to the right of which is a very young petiole still showing a circinately coiled apex. Both stem apex and young petiole are surrounded by a dense sheath of unbranched multicellular hairs. The dotted line in Text-fig. 1 indicates the extent of the hair sheath and this and the apex of the stem are also illustrated in Pl. 8, fig. 3. The transverse sections one of which is shown in Pl. 8, fig. 4, demonstrate the same feature and show that the apical tissues of the stem consist of small-celled parenchyma. It has not, however, been possible to demonstrate the existence or otherwise of a single apical cell. A section taken at a somewhat lower level where the tracheidal system is still not fully differentiated also shows that the surface hairs are present and abundant at that level (Pl. 8, fig. 5).

The branching of the stem is always unequal the stele of the daughter stem being smaller than that of the parent. In preparation for branch formation the stele becomes ovoid in section and the protoxylem group destined to supply the branch usually divides into two these passing into that part of the stele which is to form the vascular supply of the branch (Pl. 8, fig. 2). At a higher level the stele of the branch becomes separated from that of the parent stem by the inward extension of the cortical tissues the daughter stele having an oval outline as seen in transverse section with the two protoxylem groups lying one on each side of the mid-line and situated somewhat nearer the adaxial than the abaxial side (Pl. 8, fig. 1). This stage is well shown in Williamson Colln. slide 187 and is figured by Seward (1910, text-fig. 305B) and by Scott (1920, text-fig. 156A). Exceptionally the protoxylem group supplying the branch does not divide into two and occupies a median position in the branch stele. An example of this kind is figured diagrammatically

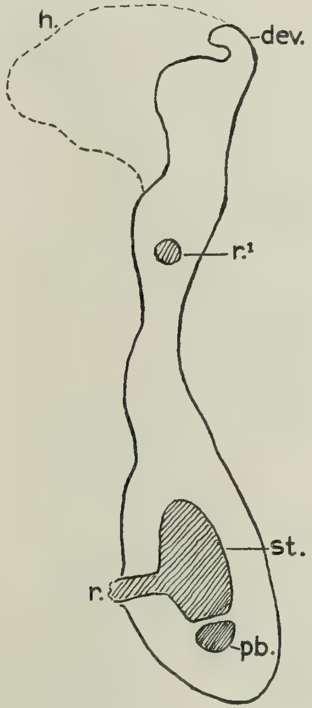


FIG. 1. *Psalixochlæna cylindrica* (Will.) Camera lucida outline of an obliquely longitudinal section passing through the stem apex. *st*, stem stele giving off petiole bundle, *pb*, and root, *r* : *r*¹, root cut transversely passing through the stem cortex : *dev*, developing petiole showing circinate vernation : *h*, dotted outline indicating extent of the hair sheath. × 12. (Holden Coll., no. 611).

by Bancroft (1915, text-fig. 1). There is some variation in the diameter of the tracheids forming the metaxylem of the branch. As a general rule these tracheids have the same dimensions as those of the parent stem but there are a number of examples (e.g. Holden Colln. 301*a*) in which they are appreciably smaller in diameter and the differentiation into small central and larger peripheral tracheids is not evident.

Petiole : The initial stages in the emission of the petiole trace bear a strong resemblance to those leading to the giving off of a branch. The assumption of the ovoid appearance of the stem stele in transverse section and the positioning of one of the stem protoxylem groups in the outgrowing metaxylem are, as far as one can judge, identical.

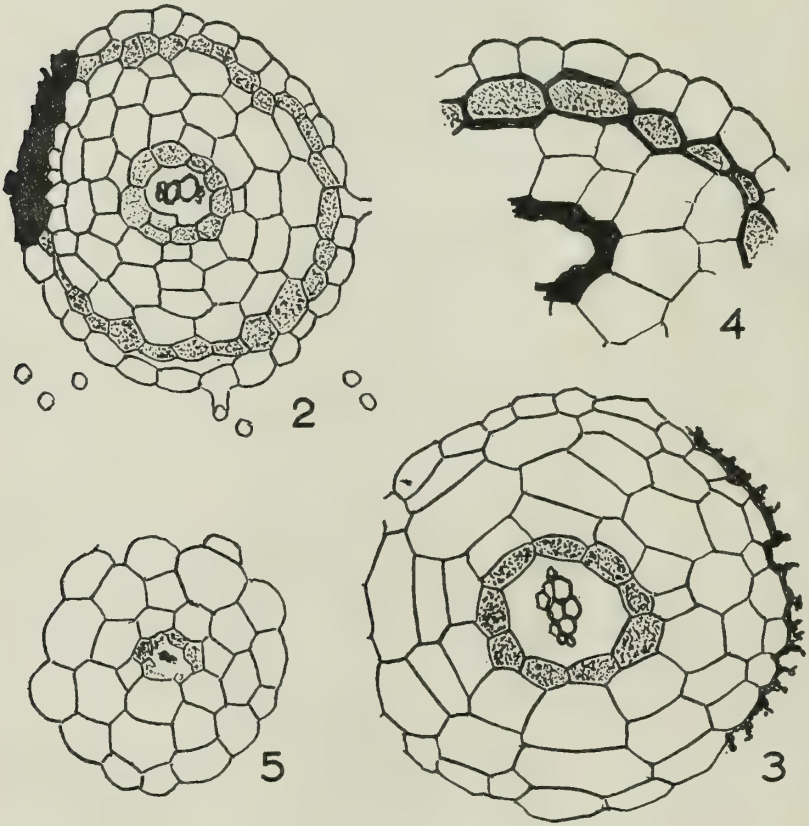
Whilst, however, the branch stele departs as a concentric structure with the protoxylem groups surrounded by metaxylem the departure of the petiole trace is heralded by the development of a strip of parenchyma on the inner side of the petiolar protoxylem. This parenchyma gradually extends to the margin of the stem stele thus separating off the petiole trace as a flattened cylinder with the protoxylem on its adaxial face. The behaviour of the protoxylem varies to some extent but it appears, in most specimens, to consist of a flattish strip of small tracheids extending discontinuously along the greater part of the adaxial face of the petiole trace. As the trace moves further out from the stem stele the protoxylem becomes divided into three definite groups though the ridges so formed do not project from the adaxial face of the metaxylem as prominently as they do in *Botryopteris ramosa* and other Coal Measure species of *Botryopteris*. Another feature which is frequently demonstrable at this stage is the greater diameter of the tracheids of the petiole trace compared with those of the parent stem. This difference in diameter which is characteristic of *Botryopteris antiqua*, *B. hirsuta* and *B. ramosa* does not, however, always occur in *Psalixochlaena cylindrica*. It is well shown in Pl. 9, figs. 1, 2, 9. In many specimens the petiole trace shows no further modification at the level of its separation from the parent axis though Bancroft (1915) mentions the fact that " there is occasionally a slight indentation on the abaxial margin of the strand ". This abaxial " indentation " is, in fact, the initial stage in the abaxial curvature of the petiole trace. It is clearly shown in Pl. 9, fig. 2 and becomes steadily more pronounced the further the petiole becomes separated from the parent stem so that, when fully established the stele has a crescentic outline as seen in transverse section with the protoxylem on the convex, adaxial side and has the shape of an inverted gutter. This abaxially curved petiole trace is clearly different from that typical of the various species of *Botryopteris* and much more nearly resembles that of *Tubicaulis*. The progressively greater extent of abaxial curvature is illustrated in Pl. 9, figs. 3, 6, 7 and culminates in the condition shown in Pl. 9, fig. 7. All the isolated petioles in the Scott Collection which are now identified with *Psalixochlaena cylindrica* were grouped by Scott in the genus *Selenochlaena*. He included his specimens under that head simply as a matter of convenience until their relationships could be established. *Selenochlaena* was a genus originally established by Corda (1845) in his revision of the fossil plants studied by Cotta (1832). Cotta's genus *Tubicaulis*, in the wide sense originally used by him, included representatives of Palaeozoic ferns which have since been transferred to other genera (e.g. *Ankyropteris* and *Etapteris*) and *Tubicaulis solenites* is the only one of those he described now recognized as a valid species. Corda's transfer of *T. solenites* to *Selenochlaena*, as Stenzel (1889) pointed out in his survey of the genus *Tubicaulis*, is invalid and he has correctly restored it to that genus.

The branching of the petiole, like its vascular supply, is characteristic and unusual. Lateral traces are given off alternately from the right and left sides of the main petiolar strand their emission commencing quite near the base of the petiole and, in some examples, beginning even before this is separated from the stem. In preparation for the emission of a branch trace a lateral protoxylem group and its associated metaxylem become detached from the margin of the main trace and, surrounded by phloem and cortical tissues, is separated from the petiole as an initially monarch secondary axis (Pl. 10, fig. 2). One such axis is figured by Bancroft (1915, text-fig. 15) who had not, however, any means of linking it positively with *Rachiopteris cylindrica*. This type of emission of the branch trace is clearly marginal in the sense proposed by Chrysler (1910) and adopted by Davie (1914) and, later by Bower (1923). Once the branch has separated from the petiole it appears invariably to dichotomize and, in some examples at least, to dichotomize repeatedly. Pl. 9, fig. 4 shows a petiole which has given off a branch to the right the vascular bundle of which is already dichotomizing whilst that destined for a branch from the left hand side of the petiole is still tenuously linked with the main petiolar strand. Pl. 10, fig. 1 shows the major part of a branch in which the vascular bundle has not only bifurcated but in which the daughter steles are again forking equally in their turn. The available evidence suggests that as the lateral protoxylems pass alternately from the petiolar stele they are renewed by the division of the central protoxylem group (Pl. 9, fig. 7).

There is no evidence of the existence of flattened assimilatory pinnae or pinnules such as those recorded in *Botryopteris americana* (Delevoryas & Morgan, 1954*b*) and in *B. forensis* (Renault, 1896) nor is there any satisfactory evidence of the type of sporangium which the plant possessed.

Root system : The roots of the first order usually arise singly from the stem although occasionally two, and exceptionally three or four, may be given off at the same level (e.g. Holden Coll. 618). Their development does not appear to bear any close relation either to the branching of the stem or to the emission of the petioles. They are always diarch with the xylem of the root stele approaching the *Osmunda* type rather than that characterizing the majority of existing leptosporangiate ferns (Pl. 10, fig. 3). As in the stem the pitting of the larger tracheids is reticulate with transversely elongated pits whilst that in the smaller ones adjoinging the protoxylem is scalariform. The thickenings of the minute protoxylem elements are spiral.

Where the xylem of root and stem unite the stem xylem is characterized by the development of a peripheral flat or slightly convex disc of small, tangentially flattened tracheids with which the expanded base of the root-xylem unites (Pl. 8, fig. 2). The roots possess a separate cortex from their point of origin the cells of which, during their passage through the stem tissues, are uniformly somewhat thick-walled and, in the majority of the specimens studied, have dense brown contents. On the emergence of the roots from the stem the thick-walled cortical cells are replaced by parenchyma although they may persist peripherally for a short time. Where the whole of the tissues of the root are preserved the superficial cells are thin-walled and develop root hairs, a feature first recorded by Bancroft. These root hairs are long and locally numerous and appear to be persistent since they are present in what are clearly mature roots (Pl. 10, fig. 4 ; Text-fig. 2). Immediately below the piliferous layer is a well-defined exodermis the cells of which have thickened walls and often possess dark contents. The stelar tissues are enclosed by a readily distinguishable endodermis (Pl. 10, fig. 3 ; Text-figs. 2–5) the cells of which, like those of the exodermis, usually have dark contents. The state of preservation of the roots, like that of the stems and petioles, is very variable. It is only rarely that the piliferous layer is present and frequently the exodermis is also represented by nothing more than a ragged fringe of broken down cell remains (Text-fig. 3). The branching of the roots is monopodial. The daughter roots and their branches are



Figs. 2–5. *Psalixochlœna cylindrica* (Will). Camera lucida drawings of transverse sections of roots.

Fig. 2. T. S. of small root in which all the tissues except the phloem are preserved : note the presence of root hairs. × 90. (Holden Coll., no. 615).

Fig. 3. A similar section in which the piliferous layer is missing and in which the exodermis, here shown in part only, is represented by a ragged fringe of cell remains. × 150. (Holden Coll., no. 301, C1).

Fig. 4. Part of a somewhat oblique section of a very small root showing the endodermis, cortex, exodermis and piliferous layer. × 200. (Scott Coll., no. 1535).

Fig. 5. T.S. of a minute root in which the piliferous layer and the exodermis have been lost. × 130. (Holden Coll., no. 301, C1).

All the figures show the large, very regular cortical cells which are characteristic of these roots.

characterized by large and very regular cortical cells which form a most distinctive feature (Text-figs. 2–5). These daughter roots were figured by Williamson (1878, pl. 24, figs. 81–85). Figures 81, 82 and 83 are described as " Transverse sections of three successively smaller stems " whilst his fig. 85 shows part of the root in fig. 83 more highly magnified. In fig. 85 the large cortical cells and the dark cells of the endodermis are clearly shown and it may be noted that both the exodermis and piliferous layer are missing. Pl. 10, fig. 4 illustrates part of a somewhat thick section showing two rootlets in which not only the endodermis and the exodermis are preserved but also the piliferous layer with numerous long root hairs. The proof that small roots such as these were part of the root system of *Psalixochlaena cylindrica* was only rendered possible by the preparation of a close series of " peels " which enabled the connection between the roots of various sizes to be established. It should be pointed out, however, that a far better picture of the root hair system is provided by the thicker hand ground specimens such as the one described above.

DISCUSSION. Before considering the light thrown on the systematic position of *Rachiopteris cylindrica* Will. by the present investigation it will be helpful to record the views of the various palaeobotanists by whom it has been mentioned. Tansley (1908) retained Williamson's name though he placed this in inverted commas. Scott (1908) also used Williamson's name but pointed out (p. 333) that whilst it had been proposed to include it in the genus *Botryopteris* its habit differed so markedly from that of other Botryopterideae that it would perhaps be preferable to establish a new genus for it. Seward (1910 : 438–440) whilst quoting Scott's opinion was the first to include the species in *Botryopteris*. It is interesting to note that, although Bancroft's paper (Bancroft, 1915) was not published until five years later, she reverted to Williamson's name though she observed that other authors had considered that the plant should be included in the genus *Botryopteris*. One of the reasons for Bancroft's retention of the name *Rachiopteris cylindrica* appears to be that her study was undertaken in the Botany Department of University College (London) which at that time was directed by the late Professor F. W. Oliver. The card index of the Oliver Collection of fossil plants has two entries dealing with the plant in question though it has not been found possible to discover which of them was first made. One of them reads " *Rachiopteris cylindrica* (generally included in *Botryopteris* but probably a different genus) " whilst the other reads " *Rachiopteris cylindrica* (inc. in Botryopt. but really diff. genus) ". It seems clear from these entries that Oliver had considerable doubts about the validity of transferring Williamson's plant to the genus *Botryopteris* and that this doubt influenced Bancroft in retaining the non-committal generic name used by Williamson.

Scott (1920 : 345–349) subsequently followed Seward's example and referred the plant to *Botryopteris* as *B. cylindrica* though obviously with some reservations. Bower (1923 : 121 ; 1926 : 10–11) and Leclercq (1925) also accepted its inclusion in *Botryopteris* as did Hirmer (1927 : 532–534) who includes it as one of the typical species of the genus. Still more recently Walton (1940 : 88–101) has also included it in his Botryopterideae among the remaining species of *Botryopteris*.

Recent discoveries in Great Britain and the United States of America strongly suggest, however, that the time is ripe for a critical re-survey of the genus *Botryopteris* and the species which at present are assigned to it. Of the British species *Botryopteris antiqua* from the Lower Carboniferous of Scotland has recently been the subject of detailed study by Surange (1952) who has added considerably to our previous knowledge of this plant though further investigation is desirable when suitable material is available. The same author (Surange, 1954) has also described under the name *Botryopteris elliptica* a rachis from the Coal Measures bearing a bud on its abaxial face. The specimen bears a close resemblance to similar buds described by Long (1943) who assigned his specimens to *B. hirsuta*. Neither Surange nor Long, however, were able to demonstrate any connection between their bud-bearing rachises and the main stems from which they had, presumably, arisen.

The comparatively brief descriptions of *Botryopteris hirsuta* and *B. ramosa* given in Scott (1908, 1920) and similarly short references in Seward (1910), Hirmer (1927) and Walton (1940) are apparently the only published sources of information on these species apart from those in Williamson's early records. Scott himself (1920 : 339) has suggested the possibility that specimens of other species had been assigned to one or other of the two named ones and it is evident that a detailed study of both species and other possibly related plants is highly desirable.

The investigation of the fossil plants from American coal balls has yielded much information about specimens of *Botryopteris* occurring in the United States. Some of these show a considerable resemblance to *B. forensis* from the French Permo-carboniferous notably that described by Darrah (1941) and later and more fully described by Delevoryas & Morgan (1954*b*). These authors correct Darrah's account (Darrah, 1941) of the method of departure of the lateral trace from the petiole strand and establish this as marginal. *B. americana*, the species described, shares with the French species, *B. forensis*, the petiole trace with its " omega-shaped " cross section and the possession of flattened pinnules as well as the stout unbranched hairs with their characteristic septa. Nothing is yet known of the stem of this species but Delevoryas & Morgan (1954*b*) suggest that the petioles and pinnules they describe may possibly represent the more distal parts of the petiolar system of the species described by Mamay & Andrews (1950) as *B. trisecta*. This species, the petiolar vascular strand of which is very similar to that of *B. americana*, possesses a stem stele which is protostelic with exarch protoxylem, a feature in which it resembles *B. forensis*. In *B. trisecta* the method of division of the primary petiole trace is very distinctive. It branches into three to form a median petiole trace which is omega-shaped in transverse section and two lateral primary pinna traces.

Whether the British and Belgian species and those of American and French origin should be included in the same genus is perhaps becoming a matter of some doubt which may only be resolved by further research as suitable specimens become available. *Psalixochlaena cylindrica* obviously shows a number of features of structural agreement with both the British Coal Measure species *Botryopteris ramosa* and *B. hirsuta* and with *B. mucilaginosa* from the Belgian Coal Measures. It shares with them a stem in which the stele has a protostelic xylem system without parenchymatous inclusions and with mesarch protoxylem, a monodesmic petiole trace with marginally produced branch traces and a superficial covering of unbranched multicellular hairs. The petiole trace is also like that of the *Botryopteris* species in possessing near its point of origin three adaxially situated protoxylem groups forming well-defined ridges on the side of the trace nearest the parent stem. *Psalixochlaena cylindrica* differs from the *Botryopteris* species in showing some differentiation of the stem stele into a median region of small tracheids surrounded by a peripheral zone of tracheids of larger calibre and in the development in the petiole trace of an abaxial curvature which gives it the form of an inverted gutter this producing a C-shaped transverse section. The abaxial curvature of the petiole trace obviously separates *P. cylindrica* from the various species of *Botryopteris* and suggests comparison with those Palaeozoic ferns which possess a similar type of trace. These are included in the three genera *Tubicaulis*, *Anachoropteris* and *Apotropteris*. Of the three genera *Tubicaulis* has been the most widely studied and includes five species namely *T. solenites* from the Permian of Saxony (Stenzel, 1889), *T. sutcliffii* from the Lower Coal Measures of Lancashire (Stopes, 1906), *T. berthieri* from the Permo-carboniferous of Autun (Bertrand, 1911) and two recently described American species, *T. multiscalariformis* from the Middle Pennsylvanian of Kansas (Delevoryas & Morgan, 1952) and *T. scandens* from the Upper Pennsylvanian of Illinois (Mamay, 1952). All these species agree in possessing a stem stele composed entirely of tracheids with exarch protoxylem and, as far as is known, a petiole trace initiated as a flat or slightly abaxially recurved bar, this developing a more pronounced abaxial curvature in its more distal parts. The protoxylem of the petiole trace appears to be distributed discontinuously along its convex, adaxial face. The place of origin of the pinna traces is not known in *T. sutcliffii* and *T. berthieri* but in the remaining three species they are extra-marginal that is, they arise from the adaxial face of the petiolar strand.

Our knowledge of the genus *Anachoropteris* is less complete, the known species, apart from *A. clavata*, being represented only by their petioles. The petiole strands of both *A. pulchra* and *A. involuta* have strongly inrolled margins whilst those of *A. clavata* (Delevoryas & Morgan, 1954) are more U-shaped in transverse section with two robust groups of comparatively large tracheids forming the arms of the U these being linked by a strip of tracheids of smaller calibre. The only stem recorded for this species is one arising from a large petiole and corresponds in type with that described by Long (1943) in *Botryopteris hirsuta*. The xylem in this stem is wholly tracheidal and the small xylem elements which occur on the periphery of the stele are interpreted as probably the protoxylem . The stele is thus exarch. In all the three species of *Anachoropteris* referred to the pinna traces are extra-marginal in origin.

It is evident that both *Tubicaulis* and *Anachoropteris* differ from *Psalixochlaena cylindrica* in the exarchy of the stem protoxylem and, where this is known, in the extra-marginal mode of departure of the pinna traces.

Apotropteris, with the single known species *A. minuta*, is a Coenopterid fern which has recently been described by Morgan & Delevoryas (1954*a*) from the Upper Pennsylvanian of Illinois. The stem stele shows a certain similarity to that of the Coal Measure plant described by Bancroft (1915) as *Rachiopteris cylindrica*, Type β. As in the latter the xylem of the stem stele is wholly tracheidal with a centrarch group of small tracheids with scalariform thickening although, in addition, other similar small tracheids occur grouped round the periphery of the stele. Morgan &

Delevoryas suggest that both the central and peripheral groups of small tracheids may be regarded as protoxylem though only the central group appears to be connected with that of the petiolar vascular supply. The latter is almost as large as that of the stem from which it arises and its emission leaves a large somewhat V-shaped depression on the side adjacent to its departure. At a slightly higher level the petiole trace becomes C-shaped as seen in transverse section with protoxylem on its convex adaxial face and with the concavity abaxial. The mode of departure of the pinna traces is not known.

It will be clear from the description of *Psalixochlaena cylindrica* Will. given in this paper and from what has been stated above that it differs in a number of features both from the various species of *Botryopteris* with which it has been previously linked and from the three genera which it resembles in possessing an abaxially curved petiole trace. A new genus, *Psalixochlaena* (from the arched vascular bundle of the petiole), is therefore instituted for its reception.

Genus ***RHABDOXYLON*** nov.

Diagnosis. A small fern with the stem densely clothed with unbranched multicellular hairs. Stelar xylem wholly tracheidal with a single centrarch protoxylem group. Cortex entirely parenchymatous consisting of an inner zone with abundant intercellular spaces and an outer zone in which these are absent. Stem branching dichotomously and equally. Petiole trace oval in transverse section with a single protoxylem group.

Type species. *Rhabdoxylon dichotomum* n. sp.

Rhabdoxylon dichotomum n. sp.

(Pl. 10, figs. 5–7)

1878 *Rachiopteris cylindrica* Williamson, p. 351, pl. 24, fig. 88
1896 *Rachiopteris cylindrica* Will.: Hick, p. 1, pl. 1, figs. 1–4, 6.
1915 *Rachiopteris cylindrica* Will. (Type β) : Bancroft, p. 532, pl. 26, figs. 3, 4, 7–9 ; pl. 27, fig. 2 ; text-fig. 8.
1920 *Botryopteris cylindrica* (Will.) (β form) : Scott, p. 347, text-fig. 157.
1925 *Botryopteris cylindrica* (Will.) (β form) : Leclercq, p. 58, pl. 47, fig. 11 ; pl. 48, fig. 12.
1927 *Botryopteris cylindrica* (Will.) (Forma β) : Hirmer, p. 533.

Holotype. A stem section (Williamson Colln. 179) figured Williamson (1878 ; 351, pl. 24, fig. 88).

Diagnosis. As for genus.

Description. The plant which Bancroft named *Rachiopteris cylindrica* Will.—Type β and which she interpreted as the marsh or sub-aquatic ecotype of the more robust Type α differs from the latter in a number of features. The stem diameter in the specimens measured ranges from 1·8 to 2·1 mm. and that of the stele from 0·35 to 0·5 mm. The xylem of the stem stele consists entirely of tracheids without any admixture of parenchyma. There is not, however, any differentiation of this into an inner zone of small tracheids and an outer zone of larger elements with the protoxylem lying at the junction between the two. The single protoxylem group occupies the centre of the xylem mass and may therefore be described as centrarch in position. The xylem is surrounded by a continuous sheath of xylem parenchyma, phloem and phloem parenchyma and the whole of the stelar tissues are enclosed in a relatively wide cortex (Pl. 10, figs. 5, 6). The tissues forming the cortex are divisible into inner and outer zones both of which are composed entirely of parenchyma. The cells of the inner zone are smaller than those of the outer one and show abundant intercellular spaces whilst those of the outer zone are more compact and are devoid of intercellular spaces (Pl. 10, fig. 5). The inner cortex frequently shows partial or complete collapse (Pl. 10, figs. 5, 6) and this may, as in one of the sections figured by Bancroft (1915, pl. 26, fig. 4) lead to the formation of large intercellular cavities separated by radial plates of collapsed parenchyma. A somewhat similar condition is figured by Leclercq (1925, pl. 47, fig. 11) in a section of the plant from Belgium though in this specimen the cavities are less regular than in the one figured by Bancroft. This type of collapse is, however, unusual and in the great majority of cases breakdown results in the formation of a dark irregular strip in which the cellular structure is difficult or impossible to distinguish. The development of large cortical cavities separated by radiating plates of tissue is not uncommon in the petrified material of plants in which the cortical tissues are divisible into a delicate parenchymatous inner part and a more resistant outer part (e.g. *Ankyropteris corrugata*, *A. westphaliensis*). In *A. corrugata* the partial breakdown of the inner cortex to form radiating plates of tissue alternating with wide cavities may take place in the plant whilst the tissues are still healthy and, where this occurs, the cells forming the radial plates of parenchyma proliferate and may partly or wholly fill the cavities (Holden, 1930, pl. 9, fig. 30 ; pl. 10, fig. 32). In other specimens of *A. corrugata* the collapse of the cortical tissues leads to no new growth and it may well be that their collapse occurred when the plant was in a moribund condition. The occurrence of similar radiating plates of parenchyma alternating with wide cavities in the inner cortex of petioles of *A. westphaliensis* was first recorded and figured by Williamson (1874, pl. 58, fig. 49) and more recently by Bertrand (1909 : 76, pl. 10, fig. 72). In none of the specimens examined by the author nor in the specimens referred to above are there any indications of cell proliferation from the radiating plates. The superficial tissues are seldom preserved but when present they develop abundant unbranched multicellular hairs. Excellent examples of these hairs or their bases are shown in Williamson Colln. slide 180, and in slides 631 and 1459 and others in the Kidston Collection. Some of these are shown in Pl. 10, fig. 7 and Text-fig. 6*a–e*. The parenchyma lying immediately below the epidermis is composed of cells which often have bright orange contents and this suggests that they may have been secretory in character.

The branching of the stem, in contrast to that of *Rachiopteris cylindrica* always leads to the formation of two equal daughter axes. The process of division is extremely simple. The centrarch protoxylem group divides into two daughter groups and these become more widely separated by the development of metaxylem tracheids between them the stele assuming an oval outline as seen in transverse section (cf. Bancroft, 1915, pl. 26, fig. 9). This stage is followed by one in which two equal centrarch daughter steles are formed (Pl. 10, fig. 6) one stele passing to each of the branches.

Petiolar formation is equally simple the stem protoxylem dividing into two and one of these passing into the vascular strand destined for the petiole. This petiolar vascular strand is ovoid in transverse section and possesses a single exarch protoxylem group on its adaxial face (Pl. 10, figs. 5–7). Usually it is much smaller than that of the stem from which it arises (Pl. 10, fig. 6; cf. Bancroft, 1915, pl. 26, figs. 3, 7, 8) though occasionally a somewhat larger example is encountered. No examples have been discovered either of the branching of the petiole or of sections showing its more distal portions so that nothing is known of these characters. The base of the petiole bears numerous unbranched multicellular hairs like those present on the stem (Pl. 10, fig. 7; Text-fig. 6*d*).

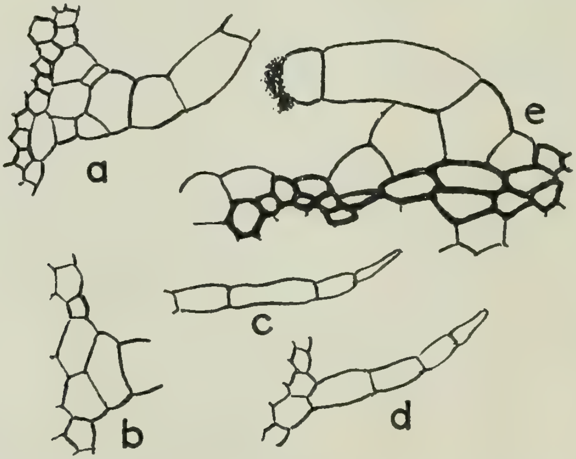


Fig. 6. *Rhabdoxylon dichotomum* n. gen. et sp. Parts of surface hairs. *a*, *b*, basal parts; *c*, tip of hair from stem; *d*, complete hair from petiole. All × 80. (Kidston Coll., no. 631): *e*, base of similar hair from stem, × 100. (Williamson Coll., no. 180).

Although Bancroft (1915) came to the conclusion that the differences between this plant and *Rachiopteris cylindrica* Will. Type α were " caused by the influence of water upon individuals " she did indicate that, among other possibilities, it might be a distinct species. The plant shares with *R. cylindrica* and with the various species at present included in the genus *Botryopteris* a stem in which the xylem consists entirely of tracheids and in which the surface is clothed with unbranched multicellular hairs. It also agrees with them in possessing a monodesmic petiole trace with adaxial protoxylem. It differs in the position of its protoxylem from both *B. forensis* and *B. trisecta* in which this is exarch, and agrees with *Apotropteris* in possessing a centrarch protoxylem though this genus, according to Delevoryas & Morgan, has small peripheral tracheids which may also be interpreted as protoxylem. The fact that no transitions have been discovered which would link *Psalixo-*

chlaena cylindrica with Bancroft's Type β apart from the rare specimens of the former in which the protoxylem of the stem is centrarch suggests that there is a good reason for placing it in a separate genus. It differs constantly in the bifurcation of the stem to form equal daughter axes, in the fact that the petiole trace has a single protoxylem group and in possessing a cortex consisting entirely of parenchyma. It is therefore proposed that an appropriate generic name for this fern is *Rhabdoxylon* (from the rod-shaped xylem of the stem) and it has been given the specific name *Rhabdoxylon dichotomum*.

SUMMARY

Psalixochlaena cylindrica (Will.) is a small fern from the Coal Measures originally assigned by Williamson (1878) to his comprehensive genus *Rachiopteris* as *R. cylindrica* and later transferred by Seward to the genus *Botryopteris* as *B. cylindrica* (Will.). It possesses a stem which branches unequally. The stem xylem consists entirely of tracheids which are differentiated into a central group of tracheids of small calibre surrounded by larger elements. The protoxylem groups, two to five in number, are situated at the junction of the large and small tracheids and are therefore mesarch in position. The cortex is divisible into three zones the inner and outer ones consisting of parenchyma whilst the middle zone is sclerized. The young parts of the stem are densely covered with unbranched multicellular hairs. The petioles, which arise singly, have a vascular supply which is monodesmic and is initially ovoid in transverse section with three adaxial protoxylem groups. In its more distal parts the petiolar vascular supply develops a pronounced abaxial curvature. Pinna traces are given off marginally and alternately from the right and left sides of the petiole trace. They are monarch and branch dichotomously. The roots are diarch with a well-defined endodermis and exodermis and with a cortex composed of very regular cells. The roots bore long root hairs which were probably persistent.

Rhabdoxylon dichotomum gen. et sp. nov. is also a small Coal Measure fern recorded from the same localities as *Psalixochlaena cylindrica*. The stem is covered with a close investment of unbranched multicellular hairs. Its stelar xylem is wholly tracheidal and possesses a single centrarch protoxylem group. The stem cortex is parenchymatous, wide in diameter and is differentiated into an inner zone of small cells with abundant intercellular spaces and an outer zone of larger cells in which there are no intercellular spaces. The stem divides into equal branches. The petioles have a vascular supply which is monodesmic and possesses a single adaxial protoxylem group. The mode of emission of the pinna traces is unknown.

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To the Photographic Department of the Museum I am indebted for the negatives and prints from which Pl. 8, fig. 1 and Pl. 9, fig. 9 have been made and to Mr. W. Anderson of the Botany Department, Glasgow University for the print represented in Pl. 9, fig. 2.

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PLATE 8

Psalixochlaena cylindrica (Will.)

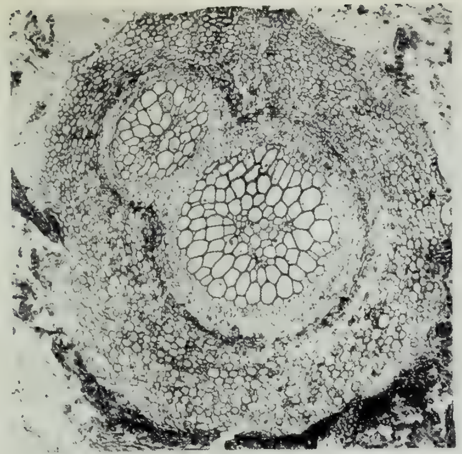
Fig. 1. T.S. of a typical section of a main stem and a branch stele with two protoxylem groups, × 25. (Holden Coll., no. 301, G76).

Fig. 2. T.S. of a stem showing an earlier stage in the emission of a branch and, to the right, the attachment of a root stele, × 35. (Holden Coll., no. 301, D2).

Fig. 3. Longitudinal section through the stem apex showing the close investment of hairs and a circinately coiled young petiole, × 60. (Holden Coll., no. 611).

Fig. 4. T.S. of the stem apex showing the investment of hairs, × 36. (Holden Coll., no. 301, D65).

Fig. 5. Part of a T.S. of a stem near the apex showing the incompletely differentiated stelar xylem and cortex and the surrounding hairs, × 20. (Holden Coll., no. 301, B94).



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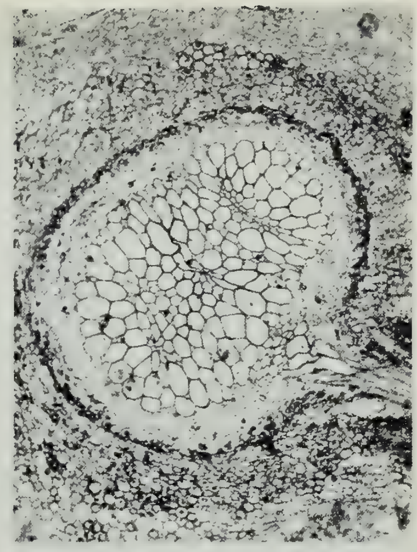

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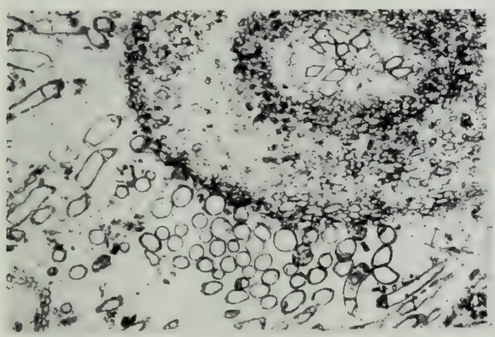

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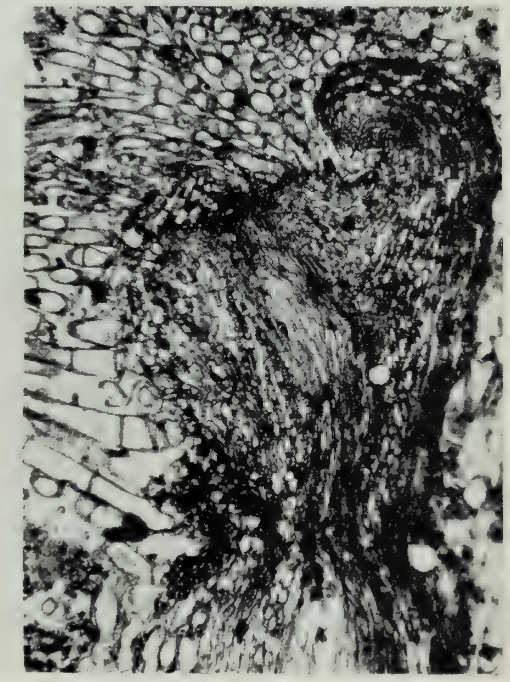

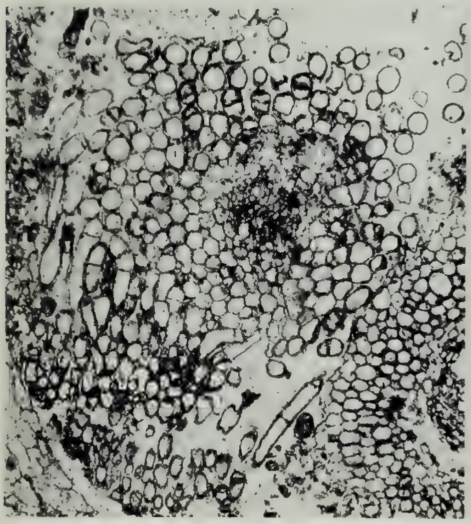

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PLATE 9

Psalixochlaena cylindrica (Will.)

FIG. 1. T.S. of a stem showing an early stage of the emission of a petiole trace, × 40. (Kidston Coll., no. 2027).

FIG. 2. T.S. section of a stem with a petiole trace to the left and a root trace to the right. Note the beginning of the abaxial curvature of the petiole trace, × 25. (Glasgow University Figd. Slide Coll., no. 595).

FIG. 3. T.S. of the vascular bundle of a petiole in which there is only a flattening of the abaxial face. The three adaxial protoxylem groups are clearly shown, × 40. (Kidston Coll., no. 2052).

FIG. 4. T.S. of petiole and pinna. The abaxial curvature of the petiole trace is more evident : the pinna trace to the left is still tenuously attached to that of the petiole : the pinna trace of the separate pinna to the right is already dichotomising, × 25. (Kidston Coll., no. 2050).

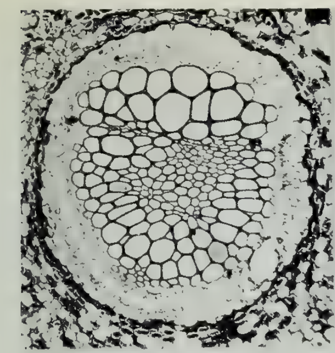
FIG. 5. T.S. of the petiole and attached pinna trace from Fig. 4 more highly magnified, × 40.

FIG. 6. T.S. of a petiolar vascular bundle showing the three adaxial protoxylem groups and a more pronounced abaxial curvature, × 60. (Holden Coll., no. 301, G76).

FIG. 7. T.S. of a petiolar bundle showing the ultimate stage of the abaxial curvature. Note that the central protoxylem group has divided, × 40. (Kidston Coll., no. 1625).

FIG. 8. T.S. of a stem showing an exceptional peripheral zone of small tracheids, × 40. (Holden Coll., no. 618).

FIG. 9. T.S. of a branch giving off a petiole trace. Note the disparity in tracheid diameter between the branch stele and that of the petiole, and the oval outline of the latter, × 25. (Holden Coll., no. 301*a*).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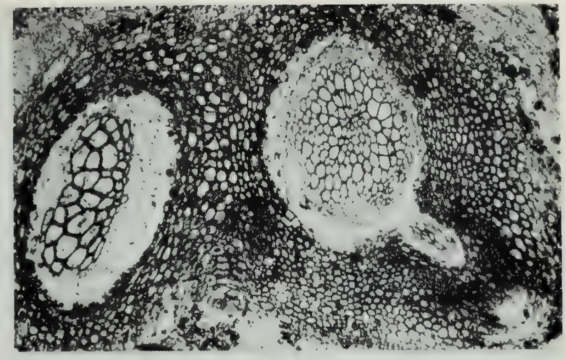
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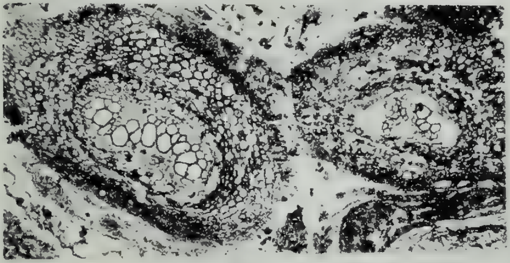
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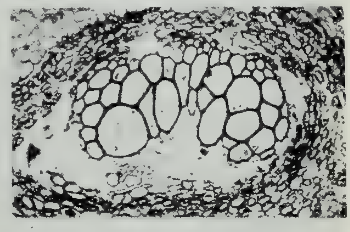
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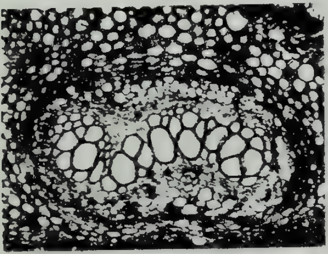
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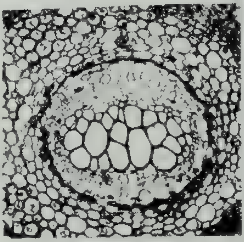
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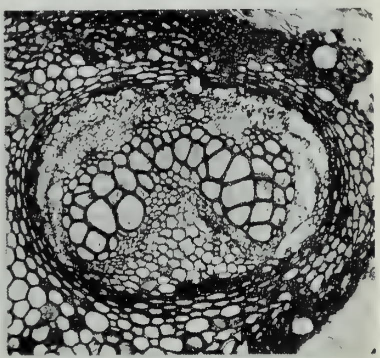
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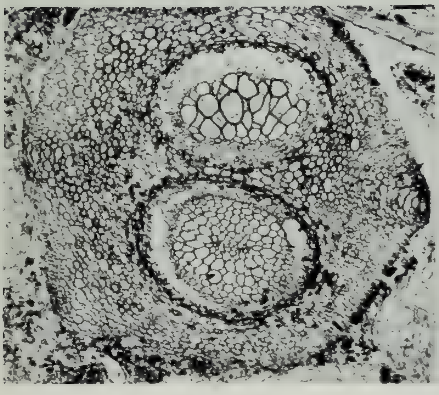
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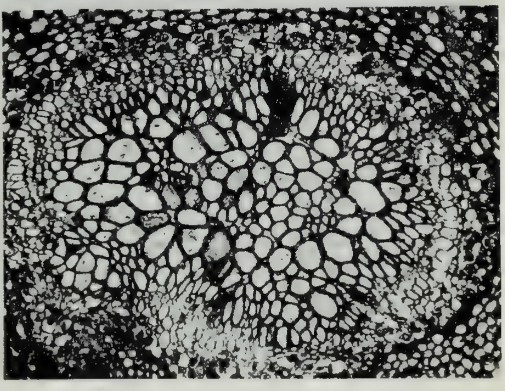
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PLATE 10

Psalixochlaena cylindrica (Will.)

FIG. 1. T.S. of a pinna trace in which the vascular bundle has dichotomised and in which the two daughter bundles are also dichotomising, × 50. (Williamson Coll., no. 178).

FIG. 2. T.S. of a monarch pinna trace, × 35. (Oliver Coll., no. K21r).

FIG. 3. T.S. of the vascular bundle of a root of the first order showing the diarch xylem and the phloem and endodermis, × 40. (Holden Coll., no. 301, B13).

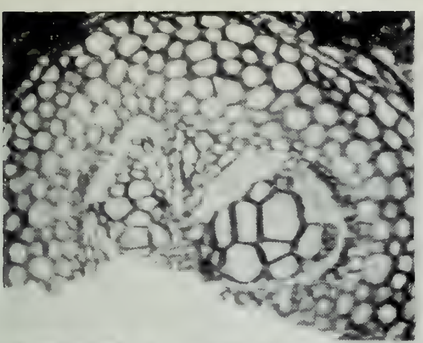
FIG. 4. T.S. of two small roots showing the piliferous layer, the exodermis and numerous root hairs, × 75. (Scott Coll., no. 1535).

Rhabdoxylon dichotomum nov. gen. et sp.

FIG. 5. T.S. of stem showing the emission of a monarch petiole trace. The loose texture of the inner cortex is well shown in the upper part of the section and its partial collapse on the sides and lower part. Note the firmer texture of the parenchymatous outer cortex, × 35. (Oliver Coll., no. K20k).

FIG. 6. T.S. of stem showing (*a*) equal forking of the stele and (*b*) the emission of a petiolar strand from the stem stele to the left of the figure, × 24. (Oliver Coll., no. K21r).

FIG. 7. T.S. of petiole showing the simple ovoid vascular bundle, the epidermis and traces of the surface hairs, × 25. (Kidston Coll., 2050).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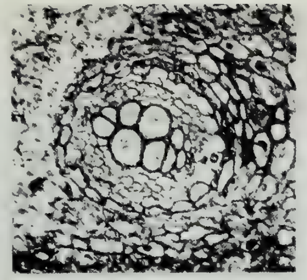
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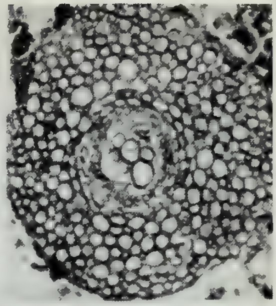
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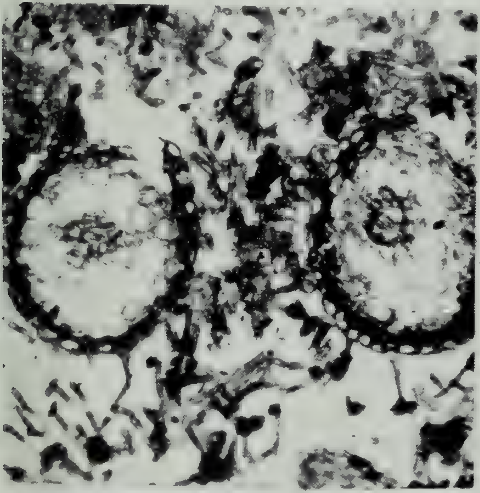
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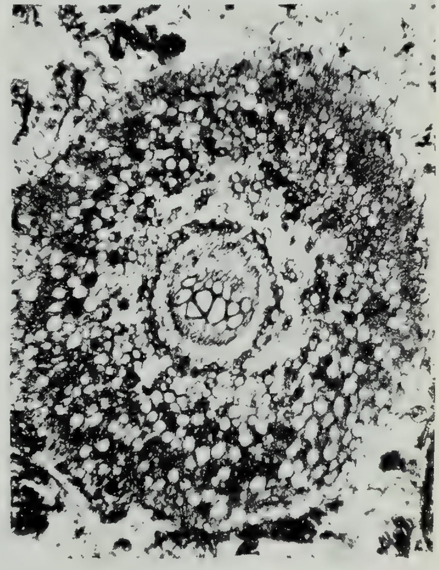
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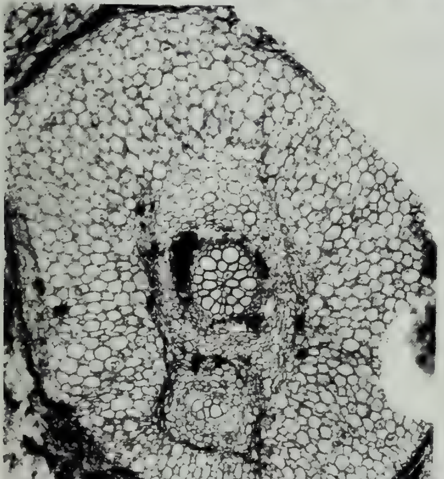
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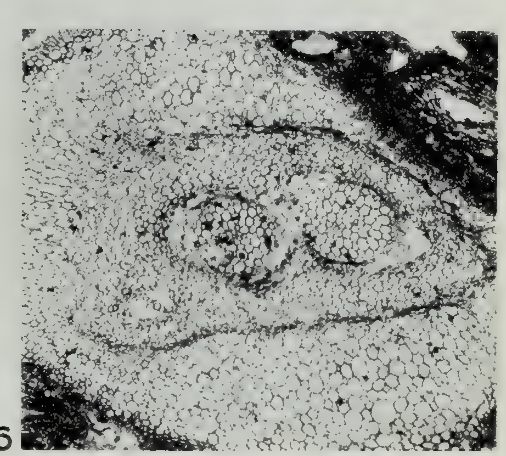
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THE ORDOVICIAN TRILOBITE FAUNAS OF SOUTH SHROPSHIRE, I

W. T. DEAN

BRITISH MUSEUM
21 APR 1960
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GEOLOGY Vol. 4 No. 4
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WILLIAM THORNTON DEAN

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Pp. 71–143 ; *Pls.* 11–19 ; 2 *Text-figures*

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THE ORDOVICIAN TRILOBITE FAUNAS OF SOUTH SHROPSHIRE, I

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SYNOPSIS

This paper is the first of four in which the trilobite faunas of the Ordovician rocks in Shropshire south-east of The Longmynd are to be described and figured. The families Raphiophoridae and Trinucleidae are dealt with first, covering a total of eight genera, of which two, *Ampyxella* and *Smeathenia*, are new, and twenty-two species. As a result of the re-examination of the Trinucleidae in south Shropshire the relationships and possible evolution of the genera concerned is discussed.

I. INTRODUCTION AND ACKNOWLEDGMENTS

THE rocks of the Caradoc Series in the type-area of south-east Shropshire have long been famous for their prolific shelly faunas. Although the brachiopods predominate numerically there is an abundant and often well-preserved trilobite fauna which has, as yet, been only partially described. In 1839 Murchison (pl. 23, fig. 9) figured what he called *Asaphus powisii* ; his illustrations of specimens attributed to the species included the cephalon of a phacopid from south Shropshire, but this error was later rectified when he referred the same cephalon to *Phacops conophthalmus* (*sic*) (1854 : 87). Also in his 1839 work Murchison (pl. 23, figs. 1 *d–f* only) employed as some of his syntypes of *Trinucleus caractaci* three cephala of the trinucleid known now as *Onnia superba* (Bancroft). Between 1846 and 1853 seven species which have been reported from south Shropshire were described or figured by both McCoy and Salter ; these included *Acidaspis caractaci*, *Calymene blumenbachi* var. *caractaci*, *Chasmops macrourus*, *Homalonotus bisulcatus*, *H. rudis*, *Lichas laxatus* and *Phacops apiculatus*.

During the remainder of the nineteenth century only one other species was added to the literature, *Ampyx pennatus* (La Touche, 1884, pl. 3, fig. 56) ; this was inadequately figured, and the exact form was unknown until revised by Reed (1932 : 205, pl. 11, figs. 5–7). In the same paper Reed erected one other Shropshire species which he named *Ampyx* (*Raphiophorus*) *edgelli*. During this same general period Bancroft (1929*a*) established several new genera and species of Trinucleidae, and although his conclusions were not at once generally accepted, subsequent research has shown many of his genera and species to be of great taxonomic and stratigraphical value.

In 1931 Shirley (p. 25, pl. 2, figs. 4–6) redescribed the type-specimens of *Calymene caractaci* Salter, and later (1936) described from Shropshire two new species, *Reacalymene pusulosa* and *Flexicalymene onniensis*, the exact distribution of these forms being then virtually unknown.

The last of Bancroft's contributions to our knowledge of the Caradoc trilobites was published in 1949, five years after his death, and although the horizons of his type-specimens were given, there was no indication of the vertical and horizontal distribution of each species. Much of Bancroft's work suffered from lack of adequate detailed diagnoses and descriptions, and even at the present day photographs of all his type-specimens have not yet been published.

Recently Whittard (1958) has described and figured from the Shelve Inlier of west Shropshire certain species of trilobites which occur also in south Shropshire, and the present writer has reviewed the stratigraphy and faunas of the type-succession (Dean, 1958).

The present work is founded essentially on trilobites contained in the Bancroft Collection, purchased by the Trustees of the British Museum (Natural History) in 1936, and on extensive collections made by the writer since the summer of 1952. The material studied comprises several hundred well-localized specimens from horizons throughout the Caradoc Series in south Shropshire. In view of the large number of species involved it has been found convenient to subdivide the work, which will appear in four parts on the basis of the included trilobite families. The present paper will deal with trilobites having a marginal suture and without the normal paired eyes, represented by the Raphiophoridae and Trinucleidae. Later it is intended to cover the proparian, gonatoparian and opisthoparian forms. In addition to the collections already mentioned others have been consulted, and I wish particularly to thank the following for permitting the examination and loan of specimens in their care: Mr. A. G. Brighton (Sedgwick Museum, Cambridge), Dr. Gunnar Henningsmoen (Paleontologisk Institut, Oslo), Dr. Valdar Jaanusson (University of Uppsala), Miss Geraldine Roche (National Museum of Ireland), Mr. J. D. D. Smith (Geological Survey & Museum) and Mr. J. T. Wattison (Shrewsbury Museum and personal collection). The research was commenced at the University of Bristol during the tenure of a Post-Graduate Research Scholarship awarded by the Shell Petroleum Co. Ltd., to whom I am grateful for financial assistance. I am much indebted to Professor W. F. Whittard, not only for supervising the initial research but also for helpful advice and discussion since that time, and for reading and criticizing the manuscript. Finally, several of the photographs have been taken by Mr. E. W. Seavill (University of Bristol), and Mr. J. Brown and Mr. P. Green (British Museum (Natural History)); to all these gentlemen I wish to express my thanks for their skill.

II. STRATIGRAPHICAL SUMMARY

The stratigraphical subdivisions of the Caradoc Series which are established on lithology alone are largely the result of the pioneer work of Salter & Aveline, Lapworth, and others. The faunal subdivisions are those proposed by Bancroft (1928, 1928*a*, 1929, 1929*a*, 1933) who erected them on trilobites and brachiopods. Recently the whole question of the succession of shelly faunas in the Caradoc Area, and their correlation with the graptolitic faunas has been reviewed in detail (Dean, 1958), and the results are summarized below. An accompanying table shows the correlation of Stages, lithological subdivisions and graptolite-zones.

The lowest Caradoc strata of south Shropshire belong to the COSTONIAN STAGE, which is equated with an as yet undetermined upper part of the Zone of *Nemagraptus gracilis* on the basis of graptolites found in intercalated shale bands in the northern part of the outcrop. In the southern Caradoc Area, at and near the type-locality of Coston, the succession, to which the name Coston Beds has been given, is essentially an arenaceous one, commencing with unfossiliferous basal conglomerates. These pass upwards into the *Harknessella* Beds, rich in brachiopods, which are followed in turn by the *Costonia ultima* Beds, massive, bedded sandstones in which the zonal trilobite is common. North of the ridge of Pre-Cambrian rocks forming the Cardington Hills the succession is more calcareous than at Coston, but again the uppermost beds are characterized by the presence of *Costonia*, though a different species.

As the result of faulting at the type-locality of Coundmoor Brook, near Cressage, the HARNAGIAN STAGE at that point includes only the lowest of the three zones usually assigned to it, that of *Reuscholithus reuschi*. The succession includes a very thin basal sandstone conformably overlying sandy Costonian beds, and a series of

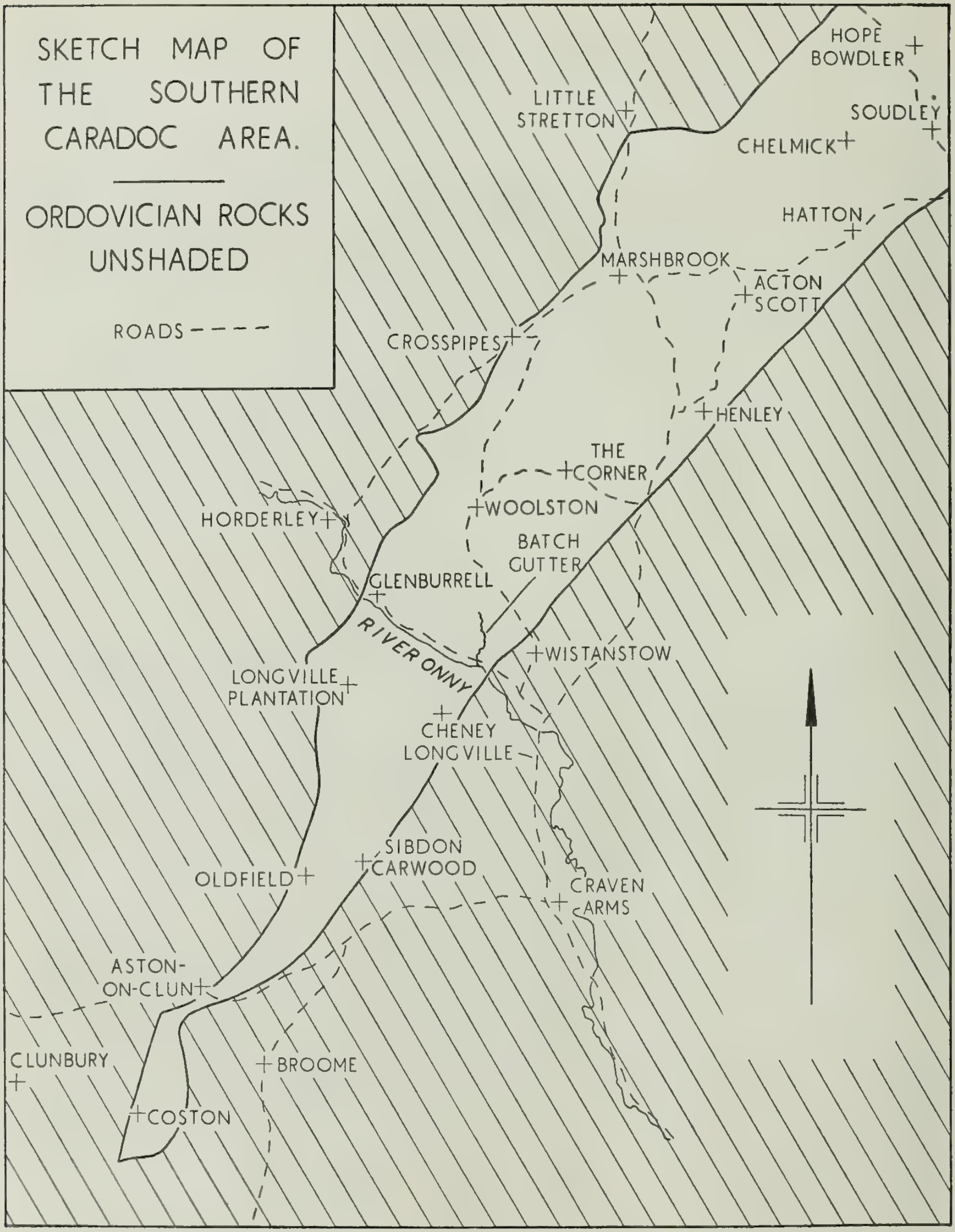
SKETCH MAP OF THE SOUTHERN CARADOC AREA.
ORDOVICIAN ROCKS UNSHADED
ROADS
HOPE BOWDLER
LITTLE STRETTON
SOUDLEY
CHELMICK
HATTON
MARSHBROOK
ACTON SCOTT
CROSSPIPES
HENLEY
THE CORNER
WOOLSTON
HORDERLEY
BATCH GUTTER
GLENBURRELL
RIVER ONNY
WISTANSTOW
LONGVILLE PLANTATION
CHENEY LONGVILLE
SIBDON CARWOOD
OLDFIELD
CRAVEN ARMS
ASTON-ON-CLUN
CLUNBURY
BROOME
COSTON

FIG. 1.

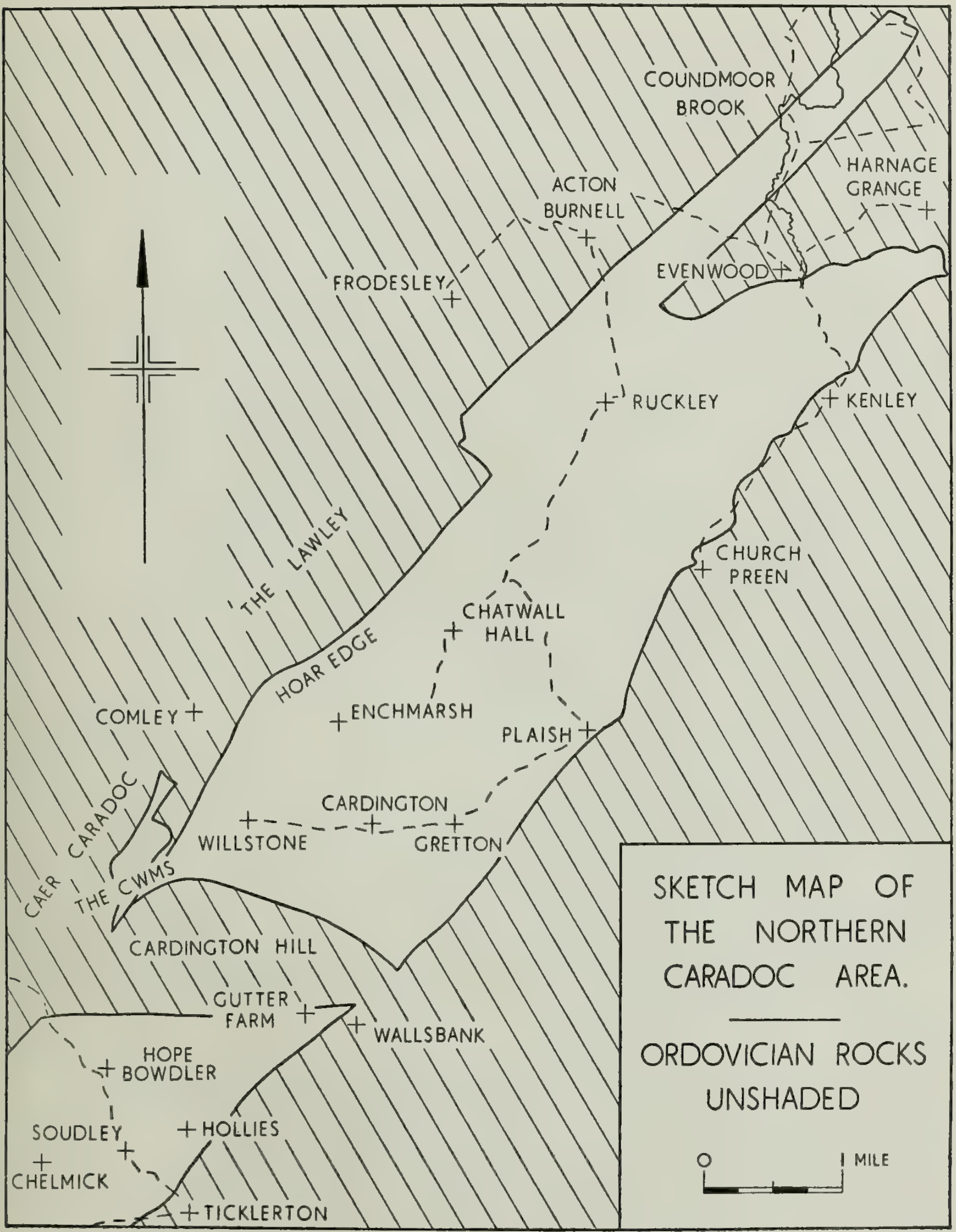
COUNDMOOR BROOK
HARNAGE GRANGE
ACTON BURNELL
FRODESLEY
EVENWOOD
RUCKLEY
KENLEY
THE LAWLEY
CHURCH PREEN
CHATWALL HALL
HOAR EDGE
ENCHMARSH
COMLEY
PLAISH
CAER CARADOC
CARDINGTON
WILLSTONE
GRETTON
THE CWMS
CARDINGTON HILL
GUTTER FARM
WALLSBANK
HOPE BOWDLER
SOUDLEY
HOLLIES
CHELMICK
TICKLERTON
SKETCH MAP OF THE NORTHERN CARADOC AREA.
ORDOVICIAN ROCKS UNSHADED
0
1 MILE

FIG. 2.

grey mudstones and shales which are the only Caradoc strata of south Shropshire to have yielded graptolites in significant numbers. Most of these beds contain, in addition to *Reuscholithus*, other trinucleids which were originally referred to *Salterolithus*, but which are now thought to be primitive members of *Broeggerolithus*. The base of the Harnagian is provisionally equated with the line separating the *Nemagraptus gracilis* and *Diplograptus multidens* Zones. To the south, at Hazler Hill, east of Church Stretton, neptunian dykes found in fissures in Pre-Cambrian rocks contain a fauna of early Harnagian age. In the Onny Valley district the Harnagian succession commences with a series of yellow, blocky mudstones, known as the Smeathen Wood Beds, which belong to the *Reuscholithus reuschi* Zone and the succeeding *Salterolithus caractaci* Zone. The Smeathen Wood Beds are followed by dark-green mudstones, the Glenburrell Beds, which have been divided into two trilobite-zones, a lower of *Ulricholithus ulrichi* (Bancroft) and an upper of *Broeggerolithus broeggeri* (Bancroft). The *U. ulrichi* Zone was retained by Bancroft in the Harnagian on account of the supposed affinity of *Ulricholithus* with *Salterolithus*, and the appearance of *Broeggerolithus* in the *B. broeggeri* Zone was said to mark the beginning of the SOUDLEYAN STAGE. Bancroft maintained that *Ulricholithus* bore no relationship to *Broeggerolithus* as typified by *B. broeggeri* but, as will be discussed in a later part of this work, *Ulricholithus* is probably best placed in the synonymy of *Broeggerolithus* and does not appear to be so closely related as was first thought to *Salterolithus*, a genus which extends with little modification upwards into the *B. broeggeri* Zone. Although trinucleids believed to belong, or be closely related, to *Broeggerolithus* occur as low as the early Harnagian it is not proposed to change the level of the dividing line between Harnagian and Soudleyan. Such a course would not serve any useful purpose, as the fauna of the newly renamed *Broeggerolithus ulrichi* Zone is imperfectly known, and in any case the drawing of the lower limit of the Soudleyan below the *B. broeggeri* Zone receives support from the available brachiopod evidence. The upper zone of the Soudleyan, that of *Broeggerolithus soudleyensis* (Bancroft), marks a change from mudstones to arenaceous strata, and is represented by the Lower Horderley Sandstone, or *Glyptocrinus* Flags, in the Onny Valley district ; farther north the same horizon is known variously as the Soudley Sandstone and the Lower Chatwall Sandstone or Chatwall Flags. Such scanty evidence as exists suggests that the junction of the Zones of *Diplograptus multidens* and *Dicranograptus clingani* may conveniently be taken between the Soudleyan and the succeeding LONGVILLIAN STAGE (Dean, 1958 : 229), but the problem has not yet been resolved sufficiently accurately.

The large vertical extent of the strata belonging to the Longvillian Stage has necessitated its subdivision into Lower and Upper Substages. The Lower Longvillian is probably confined to that part of the Caradoc Area lying to the south of the Cardington Hills, and even there it is occasionally cut out by disconformity and overstep. The fullest and best-exposed development is in the Onny Valley where the substage comprises the Middle and Upper Horderley Sandstones. These consist of brown, purple and green, massive and flaggy sandstones with impersistent lenticular limestone bands made up almost entirely of brachiopod shells. *Dalmanella* is abundant, and the species *D. horderleyensis* (Whittington), *D. indica* (Whittington) and *D. lepta*

(Bancroft), together with *Bancroftina typa* (Whittington), enable the rocks to be divided into three brachiopod zones. The trinucleid *Broeggerolithus globiceps* (Bancroft) is characteristic of the whole of the substage.

The basal member of the Upper Longvillian Substage is known as the *Alternata* Limestone, from the eponymous brachiopod *Heterorthis alternata* (J. de C. Sowerby). The strata are green, flaggy siltstones with lenticular limestone bands which die out upwards, the resulting series of uniform flaggy siltstones being known as the Lower Cheney Longville Flags. In the Onny Valley the *Alternata* Limestone follows the Upper Horderley Sandstone with apparent conformity, but farther north, at Soudley, it rests on Soudleyan beds, the Soudley Sandstone. Still farther north, beyond the Cardington Hills, it has been suggested that the Upper Chatwall Sandstone is an arenaceous facies of the basal Upper Longvillian which may again rest disconformably on Soudleyan strata (Dean, 1958 : 216). The lower part of the Upper Longvillian is characterized by the brachiopod *Kjaerina bipartita* (Salter) and the upper part by *Kjaerina geniculata* Bancroft, *K. typa* Bancroft and *Dolerorthis duftonensis* (Reed), whilst *Broeggerolithus longiceps* (Bancroft) appears to range through the substage.

The rocks constituting the MARSHBROOKIAN STAGE follow the Upper Longvillian with little change of lithology in the vicinity of the Onny Valley, where they are known as the Upper Cheney Longville Flags. *Broeggerolithus transiens* (Bancroft) is characteristic of the Stage, and the brachiopods enable the succession to be subdivided into three Zones of *Dalmanella wattsi* (Bancroft), *D. unguis* (J. de C. Sowerby) and *Onniella reuschi* Bancroft. The uppermost of these marks a transition to the ACTONIAN STAGE, an horizon which consists only of grey mudstones with thin limestones in the Onny Valley, but which includes some sandy strata, the Acton Scott Beds, farther north. *Platylichas laxatus* (McCoy) is fairly characteristic and abundant, accompanied by abundant *Chasmops*, rare *Calyptaulax*, and large numbers of brachiopods, particularly *Cryptothyris paracyclica* (Bancroft) and *Onniella* spp.

Outcrops of the succeeding ONNIAN STAGE are recorded only from the Onny Valley where they are given the name *Onnia* Beds after the contained trinucleid genus, and divided into three Zones of *Onnia*? *cobboldi* (Bancroft), *O. gracilis* (Bancroft) and *O. superba* (Bancroft). The rocks are grey and yellow mudstones, not very different from those of the Actonian, and the strata of these two Stages are believed to belong to the upper portion of the Zone of *Dicranograptus clingani*.

III. SYSTEMATIC DESCRIPTIONS

Family RAPHIOPHORIDAE Angelin, 1854

Angelin's Family Raphiophoridae was erected to include the genera *Ampyx* Dalman, *Lonchodomas* Angelin and *Raphiophorus* Angelin. Recently the type-species of these three have been redescribed by Whittington (1950) who has also included in the family the genera *Ampyxina* Ulrich and *Raymondella* Reed.

Among the Raphiophoridae recorded from the Caradoc Area is *Ampyx* (*Raphiophorus*) *edgelli* Reed, which occurs in the Actonian and Onnian Stages of the Caradoc Series. Whittington (1950 : 553) has described the type-species of *Raphiophorus* as being founded upon an unsatisfactory specimen, and has recommended that the name should not be used except for the type-species. Whether or not this course is advisable, and since then Whittard (1955 : 23) has continued to use the generic name in describing material from the Shelve Inlier, Whittington's photograph of the holotype of *Raphiophorus setirostris* Angelin shows the pygidium to be totally different from that of the Shropshire species, even though the cephalon of the Scandinavian specimen is partly crushed and therefore difficult to define.

The cephalon of Reed's species compares with that of the type-species of *Ampyx*, *A. nasutus* Dalman (Whittington, 1950, pl. 74, fig. 3), but has a median ridge running from the base of the frontal spine back to the occipital furrow. In addition, the pleural lobes of the pygidium are clearly ribbed and distinct from those of *A. nasutus* which bear only one pair of pleural furrows. At the time of Reed's description the thorax of *A.* (*R.*) *edgelli* was unknown, but recently two whole individuals have been examined, one collected by Professor Whittard (Bristol University 8312) and another in the Sedgwick Museum (A. 43831) ; each of these shows the thorax to be composed of five segments. In view of the form of the glabella, the composition of the thorax and the characteristically segmented lobes of the pygidium it is suggested that *A.* (*R.*) *edgelli* should become the type-species of a new genus for which the name AMPYXELLA is proposed.

Genus *AMPYXELLA* nov.

DIAGNOSIS. Cephalon sub-triangular in outline, with the glabella produced anteriorly to form a long spine which is quadrate and prismatic in cross-section. Median carina present on the glabella. Thorax composed of five segments of typical raphiophorid form, the first being macropleural. Pygidium subtriangular in outline. Axis tapers to the posterior extremity of the pygidium, and has numerous small axial rings which diminish in size rearwards. Pleural lobes carry an average of seven well-defined pleurae which extend outwards from the axial furrows to a small raised rim marking the margin of the pygidium.

DISTRIBUTION. The type-species has been found only in the Actonian and Onnian Stages of south Shropshire, but other forms which may possibly be referred to the new genus are recorded from as low as the Arenig Series in Scandinavia.

DISCUSSION. In addition to the type-species, *Ampyxella* possibly also includes *Ampyx latus* McCoy (1851 : 147, pl. 1E, figs. 13, 13*a*), *Ampyx volborthi* Schmidt (1894 : 80, pl. 6, figs. 11–20), a species which Skjeseth (1952 : 178) refers incorrectly to *Lonchodomas* merely on account of its having a prismatic frontal spine, and *Ampyx*? *aculeatus* Angelin (1854 : 81, pl. 40, figs. 5–5*c*).

TYPE-SPECIES. *Ampyx* (*Raphiophorus*) *edgelli* Reed, 1932.

Ampyxella edgelli (Reed)

(Pl. 11, figs. 1, 3, 4, 6 & 7)

1932. *Ampyx* (*Raphiophorus*) *edgelli* Reed, p. 207, pl. 11, figs. 1–4.
1949. *Raphiophorus edgelli* (Reed) Bancroft, p. 300, pl. 10, fig. 18.

Some details are in need of revision in the description supplied by Reed for the species. His figure of the cranidium (1932, pl. 11, fig. 1) shows the length of the glabella, from the occipital furrow to the base of the frontal spine, to be equal to the maximum breadth. Unfortunately the figured cranidium was a slightly flattened specimen and, in actual fact, the breadth is about two-thirds of the length, and the anterior portion of the glabella is almost pointed. A median ridge extends forwards from the occipital furrow as far as the front of the glabella ; at this point it appears, in plan, to divide owing to the development of a median groove which extends forwards to the tip of the frontal spine. Similar grooves are to be found on the sides and undersurface of the frontal spine, resulting in a fluted, quadrilateral cross-section.

The thorax consists of five segments, the axis being narrow, varying from rather less to rather more than one-quarter of the total breadth in uncrushed material. In a flattened specimen the axis appears somewhat broader. The side lobes are wide and flat, and the thorax attains its maximum breadth across the second and third segments. The first thoracic segment is macropleural, the anterolateral edges running obliquely backwards and outwards from the fulcral processes to the pleural points. Each pleura carries a moderately impressed pleural furrow which commences near the anterior margin at the axial furrow and then runs outwards and slighty backwards towards the pleural point. According to Reed the pygidium has five to six pleurae on each pleural lobe, but one of his figures (1932, pl. 11, fig. 4) shows a specimen with seven pleurae and this has been found to be the more usual number in the adult stage.

Horizon and localities. The cranidium, GSM. 35648, figured by Reed (1932, pl. 11, figs. 1, 1*a*) is labelled as coming from " Horderley Quarry ", but the state of preservation is such that it could only have been obtained from the *Onnia superba* Zone of the famous " Cliff Section " in the north bank of the River Onny, 720 yards west-south-west of Wistanstow Church. Of Reed's other specimens the figured pygidium GSM. 35641 (Reed, 1932, pl. 11, fig. 4) and the cited pygidium GSM. 35642 (Reed, 1932 : 208) are both labelled as deriving from the uppermost Caradoc beds of the River Onny, that is to say, the *Onnia superba* Zone. GSM. 35641 has the preservation characteristic of this horizon, but GSM. 35642 is more typical of material found in the mudstones of Actonian age which are well exposed in the bed and banks of the River Onny near the junction of Batch Gutter with the river. *Ampyxella edgelli* occurs in both the Actonian and Onnian Stages (upper part of the Zone of *Dicranograptus clingani*), but has not yet been recorded with certainty outside the general area of the Onny Valley in south Shropshire.

Lectotype (here selected). GSM. 35648 (Pl. 11, fig. 3).

Paratypes. GSM. 35641 ; GSM. 35644 ; GSM. 35646.

Figured Specimens. Sedg. Mus. A. 43831 (Pl. 11, fig. 1) ; Bristol University 8312 (Pl. 11, fig. 6) ; BM. In. 49724 (Pl. 11, fig. 4) ; BM. In. 37612 (Pl. 11, fig. 7).

Discussion. The pygidium and uncrushed cranidium of *Ampyxella edgelli* now figured bear a considerable resemblance to those described by Angelin (1854 : 81, pl. 40, figs. 5–5*c*) as *Ampyx*? *aculeatus*. The type cranidium of this species has been re-examined and figured by Thorslund (1940 : 153, pl. 9, figs. 10, 11) from the Upper *Chasmops* Limestone, Stage 4bδ, of Nakkholmen, near Oslo, but no whole individual has yet been described, and the pygidium is still imperfectly known. Until an entire specimen of this species becomes available no final decision can be made, but *Ampyxella edgelli* and *Ampyx*? *aculeatus* may prove eventually to be conspecific. The horizon of the Norwegian material corresponds broadly with that of the Shropshire specimens.

Genus ***LONCHODOMAS*** Angelin, 1854

TYPE-SPECIES. *Ampyx rostratus* Sars, 1835 by subsequent designation of Raymond (1925 : 30).

Lonchodomas pennatus (La Touche)

(Pl. 11, figs. 2, 5, 8–12)

1884. *Ampyx pennatus* La Touche, pl. 3, fig. 56.
1932. *Ampyx* (*Lonchodomas*) *pennatus* La Touche : Reed, p. 205, pl. 11, figs. 5–7.
1949. *Lonchodomas pennatus* (La Touche) Bancroft, p. 299, pl. 10, fig. 17.

The holotype, the first and only published figure of which was that given by La Touche, consists of a rather poorly-preserved cranidium, the glabella and fixed cheeks being present as an internal mould, and the underside of the frontal spine as an external mould. Reed's description (1932 : 205), founded mainly on material collected from the Onny Valley and now in the Geological Survey and Museum, gave an accurate picture of the cranidium but did not include sufficient details of the thorax, and was misleading with reference to the pygidium. A mature thorax now available (Pl. 11, fig. 8) shows the first of the thoracic segments to be slightly macropleural, the anterolateral edges running backwards and outwards from the fulcral processes to the backwardly-placed pleural ends. The equidimensional second and third segments form the widest part of the thorax which tapers hence both anteriorly and posteriorly. Apart from those of the first segment, all the pleural terminations are bluntly ended. The axis occupies roughly one-third of the total breadth, being separated from the pleural lobes by poorly-defined axial furrows. Each pleura is divided into a wide (*exsag.*) anterior band and a narrower (*exsag.*) posterior band by a pleural furrow which commences a short distance outside the axial furrow and runs outwards and slightly forwards to the pleural point, at the same time becoming deeper. The posterior margin of each axial ring is slightly convex forwards, so that a small part of the articulating half-ring of the succeeding segment is exposed.

The pygidium of the adult trilobite does not possess the angular outline described by Reed (1932 : 206) from a young specimen, and is semi-elliptical in plan, the breadth being about two and a half times the length. Reed's figure of a whole individual

(1932, pl. 11, fig. 7) is founded on a small specimen and it appears that the form of the pygidium changed during ontogeny. The axis stands higher than the pleural lobes into which it grades imperceptibly, the axial furrows being ill developed as on the thorax. Only one pair of pleural furrows is present and these follow the course of the pleural furrows of the thorax, starting just outside the axial furrows and becoming deeper until they attain the lateral margin. The border of the pygidium is steeply declined and carries terrace-lines; the remainder of the test of both thorax and pygidium is smooth. One photograph (Pl. 11, fig. 11) was taken with the test of the pygidium wet so as to show the pygidial muscle-scars. There are eight visible pairs of large, sub-oval scars, each with its long axis directed outwards and backwards, situated just inwards from the axial furrows. Between each pair of conspicuous scars is another pair of smaller, fainter scars. Sometimes similar muscle-scars are also found, faintly-impressed, on the internal mould of the glabella (Pl. 11, fig. 5). All these muscle-scars correspond with those illustrated by Whittington (1950 : 556, text-fig. 7) for *Lonchodomas rostratus* (Sars), though the pygidium of the latter species shows only six pairs of large scars.

HORIZON AND LOCALITIES. The state of preservation of La Touche's holotype, as a limonitic mould in an ochreous-weathering mudstone, associated with " *Rafinesquina* " *holli* (Davidson), shows that the specimen must have been collected from the beds of the Onnian Stage, *Onnia superba* Zone, such as are exposed at the " Cliff Section " in the north bank of the River Onny 720 yards west-south-west of Wistanstow Church. In south Shropshire *Lonchodomas pennatus* appears first in the lowest beds of the Actonian Stage, and is not uncommon both there and in the succeeding *Onnia*? *cobboldi* and *Onnia gracilis* Zones, particularly the latter, of the Onnian. The species occurs also in the Onnian of the Cross Fell Inlier.

HOLOTYPE. BM. In. 37621 (Pl. 11, fig. 12).

OTHER SPECIMENS. BM. In. 48561 (Pl. 11, figs. 2, 5); BM. In. 48935 (Pl. 11, fig. 8); BM. In. 48934 (Pl. 11, figs. 9, 11); BM. In. 48939 (Pl. 11, fig. 10).

DISCUSSION. The specific name *pennatus* as applied to this form was originally used by Salter as an unpublished manuscript name for the species which is now known as *Ampyxella edgelli*. The Shropshire trilobite bears an obvious resemblance to *Lonchodomas rostratus* Sars sp. (Størmer, 1940 : 128, pl. 2, figs. 1–4) from the *Ampyx* Limestone, Zone of *Nemagraptus gracilis*, of the Oslo region, Norway, but the glabella of the latter species is slimmer with a slightly-developed median ridge or carina which diminishes posteriorly, and the pygidium is proportionately shorter with two pairs of pleural furrows instead of one.

The cranidium of *Lonchodomas politus* (Raymond, 1925 : 39, pl. 2, figs. 8–9 only; Cooper, 1953 : 18, pl. 6, figs. 1, 2, 5–10), though possessing a test partly covered with coarse punctae, is generally similar to that of *L. pennatus*, but the pygidium of the North American species is noticeably different, being shorter and more distinctly segmented. *Lonchodomas punctatus* (Cooper, 1953 : 18, pl. 4, figs. 20, 21) possesses a pygidium which is very close, both in outline and segmentation, to that of *L. pennatus*, but as no other part of the exoskeleton has been figured it is not possible to make a detailed comparison. Both these North American forms are from the Black River Stage of Tennessee.

Family Trinucleidae Hawle & Corda, 1847

Until Bancroft's work on the separation of new genera of trinucleid trilobites the only names in general use were *Trinucleus*, *Cryptolithus* and *Tretaspis*, and some disagreement existed as to whether the first two of these were synonymous one with the other. Reed (1912, 1912*a*) disregarded to a large extent the pitting of the cephalic fringe, though discussing its structure, and stressed the form of the glabella and glabellar furrows. Bancroft (1929*a*) also considered these criteria, but emphasized the importance of the fringe pits in classification. In his work on the Scandinavian Trinucleidae Størmer (1930) rejected most of Bancroft's genera established on fringe characters but later (1945) partly retracted his criticisms, though only to the extent of accepting the names as possible sub-genera within *Cryptolithus*. Whittington (1940) refuted Størmer's contentions and followed Bancroft in stressing the importance of the form and pattern of the cephalic fringe. In a later paper (1941) he repeated this argument and, in a review of trinucleid classification, retained all the valid genera proposed by Bancroft ; *Ulricholithus* Bancroft, 1933 was at that time invalid and remained so until 1949. All the genera found in south Shropshire were placed in the subfamily Cryptolithinae, following Bancroft, but some of these forms differ so markedly from *Cryptolithus* (*s.s.*) in fringe pattern that the establishment of further subfamilies will probably be necessary, though the present state of knowledge is insufficient to attempt this satisfactorily.

More recently Whittard (1955 ; 1956 ; 1958) has followed the lines of attack set out by Bancroft and erected several new trinucleid genera, all of pre-Caradoc age, which, like the south Shropshire forms, have proved to be of great stratigraphical value. He has also proposed a modified form of Bancroft's notation for the fringe pattern whereby any particular pit can now be represented by a formula. Whilst this has proved particularly useful in the case of earlier Ordovician Trinucleidae with a simpler pit arrangement, it is often more difficult to apply it to all Caradoc forms with equal success owing to the more elaborate pattern, and in certain cases it has been found convenient to return to what is virtually Bancroft's original method.

Any modern account of trinucleid trilobites must consider not only the arrangement and relative size of the pits of the cephalic fringe as well as the position of the girder, but also other factors such as the outline and form of the cephalon, the form of the glabella and glabellar furrows, the type of pygidium, and the occasional presence of raised ridges between radial rows of pits. Whittard (1958 : 84) has questioned the validity of the last of these features, claiming that such interradial ridges may be the result of a different environment, but this argument lacks conviction as the ridges have been found to persist in certain species of *Broeggerolithus* preserved in mudstone, limestone and sandstone environments, and they are useful for at least specific discrimination. Their development can be traced in *Broeggerolithus*, in which they appear markedly for the first time.

The reticulation of the test in trinucleids has been accepted as a feature of importance by Bancroft (1933 : 2 ; 1949 : 295) ; he used its absence as one of the diagnostic features of his genus *Ulricholithus* (here placed in the synonymy of *Broeg-*

gerolithus), and attributed its absence to the effects of a deep, muddy environment (1949 : 297). Further examination of the south Shropshire material shows that, generally speaking, most trinucleids bear reticulation on the surface of the glabella and cheeks during the early stages of their development, in both limestone and mudstone environments. This is usually apparent when the original test or its impression is preserved, but the reticulation may not survive the limonitic replacement of the test. In most cases it disappears by the time the adult stage of development is reached, but may sometimes be retained as, for example, in certain specimens of *Broeggerolithus longiceps* (Bancroft) and *B. transiens* (Bancroft). In one case a small holaspid of *Reuscholithus reuschi* Bancroft, 11 mm. broad, shows relict traces of reticulation, not only on the posterior part of the cephalon but also on the thoracic segments. Rarely a single slab of rock may contain specimens of one species, apparently at the same stage of development, of which one has a smooth test whilst another adjacent to it has reticulate cheek-lobes and glabella.

Størmer (1930) published graphs showing the variation in the number of pits present at different points of the cephalon in certain Trinucleidae, particularly *Tretaspis*; the pits included were *a*. those along the rear margin of the fringe, *b*. the number of rows in front of the glabella at its mid-point, and *c*. the number of rows in front of the axial furrows. The range of variation, especially of *b*. and *c*. was not usually very great. More recently Cave (1957) has shown the greater variation in the number of fringe pits present in the species *Salterolithus caractaci* (Murchison) at one horizon in the Caradoc Series of Welshpool. In the present work an attempt has been made to indicate the variation in the number of pits found in certain species from Shropshire, but this has only been attempted in cases where the number of specimens is considered sufficiently large.

In spite of the criticism engendered by Bancroft's " splitting " of the Trinucleidae into numerous genera, it becomes obvious after examination of large-scale collections that the number of available generic names is not yet sufficient, and that at least one more must be erected to contain only those species found in the Caradoc Series of south Shropshire. The question of the relationships of the Trinucleidae is complex, and will not be made easier by attempting to extend the scope of existing genera beyond reasonable limits, such a course tending to suggest close affinities which may not, in fact, exist. In the present work the following genera are recognized :

Costonia Whittard, 1956. Type-species : *Marrolithus ultimus* Bancroft, 1949. Geological range : uppermost Costonian. Distribution : known only from south Shropshire.

Reuscholithus Bancroft, 1929. Type-species : *Reuscholithus reuschi* Bancroft, 1929. Geological range : lowest Harnagian. Distribution : known only from south Shropshire.

Smeathenia gen. nov. Type-species : *Salterolithus smeathenensis* Bancroft, 1949. A detailed description and diagnosis will be found later in this paper. Geological range : lowest Harnagian. Distribution : known only from the southern part of the Caradoc Area, south Shropshire.

Salterolithus Bancroft, 1929. Type-species : *Trinucleus caractaci* Murchison, 1839. Geological range and distribution : in south Shropshire the genus appears early in the Harnagian Stage, and ranges upwards into the *Broeggerolithus broeggeri* Zone of the Soudleyan. A similar range is known from the Shelve Inlier, the Welshpool District and, perhaps, Central Wales.

Broeggerolithus Lamont, 1935 *ex* Bancroft MS. Type-species: *Cryptolithus broeggeri* Bancroft, 1929. As already stated, *Ulricholithus* Bancroft, 1949 (type-species: *Salterolithus* (*Ulricholithus*) *ulrichi* Bancroft, 1949) is considered here to be synonymous with *Broeggerolithus*, thus necessitating a slight modification of the definition of the lower limit of the Soudleyan Stage (see page 000). Geological range: the appearance of *Broeggerolithus* was thought to indicate the beginning of the Soudleyan Stage, but the species originally described as *Salterolithus harnagensis* Bancroft, from the lowest zone of the Harnagian, is here interpreted as being a primitive member of *Broeggerolithus*, possibly linked to the typical *B. broeggeri* by forms such as *Broeggerolithus* [*Ulricholithus*] *ulrichi* (Bancroft). The genus ranges through at least to the end of the Marshbrookian, but evidence of its existence in the Actonian, either in south Shropshire or the Cross Fell Inlier, is not yet satisfactorily established. One of the most abundant and widespread of all trinucleid genera *Broeggerolithus* is known from south and west Shropshire, most parts of North Wales, Central Wales, the Cross Fell Inlier, the Dry Gill area of the northern Lake District, and perhaps also southern Norway and Sweden.

Onnia Bancroft, 1933. Type-species: *Cryptolithus superbus* Bancroft, 1929. Geological range and distribution: in the Anglo-Welsh area the genus is confined to the Onnian Stage of south Shropshire, the Welshpool district and the Cross Fell Inlier, but may occur slightly later in southern Norway. A record of *Onnia* from Venezuela is certainly incorrect, but the genus occurs abundantly in European Middle Ordovician faunas of Bohemian affinities.

Genus ***COSTONIA*** Whittard, 1956

DIAGNOSIS: Cephalon with sub-rounded anterolateral angles. Fringe carries one row of pits external to the girder, except in front of the glabella, where there may be up to twelve adventitious pits, forming what is virtually the beginning of an E_2 row. The pits of E_1 become distended at the anterolateral angles in the adult form. Pygidium is short, with curved posterior margin, and the segments of the pleural lobes are poorly defined.

DISCUSSION. The genus was erected by Whittard to include those *Marrolithus*-like trinucleids in which an E_2 row of up to about twelve pits is developed in front of the glabella. *Costonia* appears to be restricted in its vertical range to the topmost beds of the Costonian Stage where it constitutes a useful zonal index. The genus is not yet known outside south Shropshire where *Costonia ultima* (Bancroft) and *C. elegans* sp. nov. are apparently characteristic of the southern and northern parts respectively of the Caradoc Area; these districts correspond, at least in a general way, with those portions of the type Caradoc Series which crop out to the south and north of the Cardington Hills, east of Church Stretton.

TYPE-SPECIES. *Marrolithus ultimus* Bancroft, 1949 by original designation of Whittard (1956: 50).

Costonia ultima (Bancroft)

(Pl. 12, figs. 1–12)

1949. *Marrolithus ultimus* Bancroft, p. 297, pl. 9, fig. 7.
1956. *Costonia ultima* (Bancroft) Whittard, p. 50.
1958. *Costonia ultima* (Bancroft) : Dean, pl. 26, figs. 1, 2.

Bancroft's holotype, In. 43489 (Pl. 12, fig. 10), is a fragment, rather less than half, of the external mould of a cephalon estimated to have been about 7 to 8 mm. in length, and was figured in the form of a gutta-percha cast. The specimen does not show the development of E_2 pits characteristic of the genus, and though the pygidium was described briefly it was not figured, nor was any specimen in the Bancroft Collection singled out as type-material. Well-preserved topotypes are not easy to obtain, and the following detailed description is founded on mainly fragmentary specimens collected from decalcified massive sandstones.

The complete exoskeleton, excluding the genal spines, is slightly longer than wide. In one such example the maximum breadth of the cephalon is 17 mm. and the total length, including thorax and pygidium only, is 19 mm.; the overall length of the same entire specimen, including the broken-off genal spines, is at least 21 mm. The cephalon is almost subrectangular in outline and moderately convex, its length, excluding the occipital spine and genal spines, being rather more than half the maximum breadth. The glabella is long, moderately convex and tapering posteriorly, standing higher and extending forwards farther than the plump cheek-lobes. The axial furrows are deep and broad, slightly convex outwards, with small hypostomal pits situated anteriorly. In some internal moulds a pair of poorly-defined glabellar furrows is seen delimiting a pair of small, basal glabellar lobes. The occipital furrow is shallow and transversely straight, ending laterally in a pair of slot-like apodemal pits ; the occipital ring is short (*sag.*) and produced into an inclined occipital spine, the combined length of the two being just over half that of the glabella. The pleuroccipital furrow is straight and moderately deep, marking-off the narrow (*exsag.*) posterior border which continues transversely straight as far as the fulcral sockets where it is turned backwards slightly towards the genal angles. The cephalic fringe is declined gently in front of the glabella and more steeply at the sides ; the posterolateral portions of the lower lamella of the fringe are produced into long genal spines, each prismatic and longitudinally grooved, which are noticeably splayed. The median part of the frontal margin is slightly convex forwards, resulting in a bluntly-pointed appearance, the lateral margins are slightly convergent forwards, and the anterolateral portions of the fringe are moderately obtuse. There are four concentric rows of pits present in front of the glabella, of which the outermost, E_2, consists merely of eight to twelve pits arranged in such an irregular manner that they cannot satisfactorily be placed in the fringe formula. Usually E_2 extends on either side of the sagittal line as far as R4 or R5. The remainder of the fringe formula of an average cephalon is E_1 1–23 or 24 ; e_1 xix ; I_1 1–25, I_2 1–21 (beyond which point the radial arrangement ceases), I_3 3 or 4–24, I_4 6 or 7–24. Over much of the fringe both concentric and radial arrangement of pits is conspicuous, but beyond R19 to R21 the radial arrangement is continued only in I_1 and E_1. The pits of I_1 and I_2 are almost equal in size, and larger than those of other rows ; in some specimens there may be some inflation of the fringe centred on pits I_1 12–15 or 16. There are usually 10 or 11 pits situated along the posterior fringe margin which is directed outwards and slightly backwards, and is gently convex posteriorly. No well-preserved specimen has yet been found showing the underside of the fringe, but external moulds indicate that the girder is not particularly well developed, though becoming stronger just before reaching the genal angle. There is a pseudogirder between I_3 and I_4, which are farther apart than the other concentric rows, but it is only developed in the anterolateral parts of the fringe (Pl. 2, figs. 2, 5).

The thorax consists of six segments of typical trinucleid form, the first being macropleural with its anterolateral edges running sharply backwards and outwards from the fulcral processes to the pleural points. The axis of each segment, standing only slightly higher than the side lobes, occupies roughly one-quarter of the total breadth, and, in the internal mould, has two pairs of apodemal pits. The first and larger pits are situated in the articulating furrow just inwards from the axial furrows ; the second pair is situated slightly to the rear of the first, in the axial furrows themselves and just in front of the posterior margin of the segment. Each pleura carries a pleural furrow which runs outwards and slightly backwards from just outside the axial furrow to the backwardly-directed pleural point, at the same time becoming noticeably deeper. Each pleural furrow divides the pleura into a posterior and an anterior band, of which the former is the wider (*exsag.*).

The pygidium is semi-elliptical in plan, the breadth about three times the length. There is a slightly-raised marginal ridge, and the border is steeply declined. The axis is better defined in the internal than in the external mould, occupying between one-quarter and one-fifth of the maximum breadth and carrying one axial ring. The axial furrows are poorly defined on the external mould, and the side-lobes are almost smooth, but there is a suggestion of two pairs of pleural furrows near the lateral margins.

HORIZON AND LOCALITIES. The type-locality is the disused quarry about 500 feet south of Coston farmhouse, one mile east of Clunbury, but the species also occurs abundantly at the old quarry in Brokenstones Plantation 1600 yards north-east of Horderley Station. *Costonia ultima* has also been found at the small quarry by the east side of the barn 400 yards north of Glenburrell Farm, Horderley, and at the now overgrown quarry 650 yards west of Woolston House, Woolston. All these localities are in the topmost part of the Costonian Stage of the southern Caradoc Area, in strata to which the names *Horderleyella plicata* Zone, Upper Coston Beds and *Costonia ultima* Beds have variously been applied (Dean, 1958 : 197).

HOLOTYPE. BM. In. 43489 (Pl. 12, fig. 10).

OTHER SPECIMENS. BM. In. 54031 (Pl. 12, figs. 1, 3) ; BM. In. 48942 (Pl. 12, fig. 4) ; BM. In. 54033 (Pl. 12, fig. 7) ; BM. In. 54036 (Pl. 12, figs. 2, 5) ; BM. In. 48940 (Pl. 12, fig. 8) ; BM. In. 54032 (Pl. 12, fig. 9) ; BM. In. 54034 (Pl. 12, fig. 11) ; BM. In. 48941 (Pl. 12, fig. 12) ; BM. In. 54035 (Pl. 12, fig. 6).

DISCUSSION. Apparently Bancroft named his species *Marrolithus ultimus* in the belief that he was, in fact, dealing with the last known form of *Marrolithus*, and in his Correlation Tables (1933 : Table 3) he equated the Spy Wood Grit with the Hoar Edge Grit of the Caradoc Area on the grounds that it contained what he called "*Marrolithus* (Costonian type)". However, Whittard (1955 : 5 ; 1956 : 60–63) has shown more recently that the Spy Wood Grit belongs to the *Diplograptus multidens* Zone, so that it must therefore be younger than the Costonian, and that all the trinucleids known from the horizon may be referred to *Marrolithus* (*s.s.*). None of these species bears any resemblance to *Costonia* which is easily distinguished by its anterior development of E_2 pits and which, so far as is now known, is restricted to the Caradoc Area.

Costonia elegans sp. nov.

(Pl. 13, figs. 1–6, 8, 9)

1938. *Trinucleus* (*Cryptolithus*) aff. *favus* Salter : Stubblefield *in* Pocock *et al.*, p. 256.
1956. *Costonia* sp. nov. Dean *in* Whittard, p. 50.
1958. *Costonia* sp. nov. Dean, pp. 198, 218.

DESCRIPTION. The cephalon is moderately convex longitudinally and strongly convex transversely, its length, excluding genal spines, being about two-thirds of the breadth. The anterior border is gently convex, particularly medially, and the lateral margins are straight and convergent anteriorly. The glabella is moderately convex, with a small median ocellus, and extends slightly forwards in front of the cheek lobes, from which it is separated by broad, shallow axial furrows containing small hypostomal pits. Glabellar furrows are present only as two, or perhaps three, pairs of poorly-defined depressions which probably represent the position of muscle-scars. The occipital ring is transversely convex, and produced into a stout occipital spine directed upwards and backwards. The pleuroccipital furrows and pleuroccipital segment are markedly straight transversely as far as the fulcral sockets, but beyond these the posterior margin curves strongly backwards and then outwards to the genal angles. The test is frequently preserved and, in the adult, quite smooth, though a fragment of the cheek-lobe of a small individual (Pl. 13, fig. 9), estimated breadth about 5 mm., is strongly reticulate. In front of the glabella the fringe is moderately declined, becoming almost flat near the anterior border ; the lateral portions of the fringe are steeply declined. There are four continuous rows of pits, E_1 and I_{1-3}, and E_2 is developed to the extent of up to a total of 18 pits which may extend as far as R9 on either side of the sagittal line. E_1 consists of 34 small pits in the holotype, but I_1 comprises 23 larger pits, including a number of inflated ones at the anterolateral angles. The pits of I_2 and I_3 are small, numbering 26 and 22 respectively, whilst I_4 consists of 20 pits of similar size and extends from R5 or the line of the axial furrow. The 20 pits of I_5 are smaller, developed only from R6 or R7, and I_6 includes only 6 or 7 pits at the posterolateral angle of the cheek-lobe. Many of the pits have a conspicuous radial arrangement, and nineteen radii can be counted but beyond this point numerous auxiliary pits are added and the radial pattern is lost in a complex of pits. The notation for the principal rows of the fringe of the holotype, as far as the radial pattern persists, is E_1 1–20 ; E_2 1–7, 9 ; e_1 ii, iv, v, viii, ix, xiii ; e_2 0, i, iii ; I_1 1–21 ; I_2 1–22 ; I_3 4–22 ; i_2 vi, xix ; i_3 x. The area of inflated pits at the anterolateral angles is restricted in comparison with that usually found developed in *Marrolithus* (*s.s.*), and includes only pits of I_1 ; according to the notation proposed by Williams (1948 : 68–70) the inflated area is represented by the formula $CA71_1$, but using the more generally applicable method of Whittard this becomes I_1 10–16. The genal spines are not completely known but appear to curve outwards and backwards from the genal angles ; they arise in advance of the rearmost part of the posterior margin, which is strongly convex posteriorly and forms fairly large " ears ".

The thorax is unknown.

The pygidium is bluntly pointed posteriorly, the posterolateral margins being gently curved or slightly subangular. The breadth is roughly three times the length, and the border is steeply declined for the most part, becoming less so at the posterior termination. The axis is narrow, about one-sixth of the total breadth, and the axial rings number about 10 or 11 ; the first six ring furrows are continued on to the generally flat side-lobes as six fairly well-defined pleural furrows which become slightly sigmoidal towards the margins.

Comparatively little is known of the development of *Costonia elegans*, but no anterolateral development of inflated pits in I_1 has yet been found in cephala up to 12 mm. in breadth. As stated earlier, a fragment of an immature cheek-lobe, in common with those of numerous other Trinucleidae, shows reticulation which disappears by the time the adult stage is reached.

HORIZON AND LOCALITIES. The species occurs fairly abundantly at one horizon, the sandy limestones with *Harknessella subquadrata* Bancroft which constitute the topmost local subdivision of the Costonian throughout the northern part of the Caradoc Area of south Shropshire. *C. elegans* has not yet been found outside the northern Caradoc Area, and the strata for which it is the characteristic fossil are believed to be represented farther south by more arenaceous beds containing another species of *Costonia*, *C. ultima* (Bancroft). With the exception of one specimen, In. 49728, all the type material is from the old quarry in the north-eastern part of Round Nursery, 1,380 feet south-east of Harnage Grange, the remaining paratype being collected from the upper beds of the disused quarry at the eastern end of Black Dick's Coppice, Evenwood. The new species occurs also at the Bullhill " gutter-section ", Evenwood, and at the disused quarry in The Cwms, east of Church Stretton.

HOLOTYPE. BM. In. 49744 (Pl. 13, figs. 1, 2, 4).

PARATYPES. BM. In. 49733 (Pl. 13, fig. 3) ; BM. In. 49746 (Pl. 13, fig. 9) ; BM. In. 49747 (Pl. 13, fig. 6) ; BM. In. 49311 (Pl. 13, fig. 8) ; BM. In. 49745 (Pl. 13, fig. 5).

DISCUSSION. *Costonia elegans* differs from *C. ultima* (Bancroft), the only other described species of the genus, in having a greater development of E_2 in front of the glabella and a much larger number of pits with a random arrangement at and near the genal flanges, in the conspicuous rearward convexity of the posterior margin of the fringe, and in the less rounded outline of the pygidium. Our knowledge of the last of these is established as yet, however, only on immature material, and it is possible that the outline of the pygidium may change during ontogeny. The new species is important in that it appears to mark a transition, both morphological and stratigraphical, between the genera *Marrolithus* and *Reuscholithus*. The inflated anterolateral areas of the fringe are particularly characteristic of *Marrolithus*, but the outline of the cephalon, the forward position of the genal spines and the numerous random pits are more typical of *Reuscholithus*.

Genus ***REUSCHOLITHUS*** Bancroft, 1929

This so far mono-specific genus is confined to the lowest trilobite-zone, to which it gives its name, of the Harnagian Stage in south Shropshire, and has not yet been found outside the Caradoc Area.

TYPE-SPECIES. *Reuscholithus reuschi* by original designation of Bancroft (1929*a* : 78).

Reuscholithus reuschi Bancroft

(Pl. 14, figs. 1–14)

1929*a*. *Reuscholithus reuschi* Bancroft, p. 82, pl. 1, figs. 3–5.
1938. *Trinucleus* (*Cryptolithus*) *reuschi* (Bancroft) Stubblefield *in* Pocock *et al.*, p. 256.
1949. *Reuscholithus reuschi* Bancroft : Bancroft, p. 297, pl. 9, fig. 3.
1958. *Reuscholithus reuschi* Bancroft : Dean, pl. 26, fig. 3.

DESCRIPTION. The cephalon is moderately convex, bluntly rounded to broadly pointed in front. The anterolateral margins may be subangular or rounded, the straight sides being slightly convergent anteriorly. Generally speaking, the ratio of length to breadth for the cephalon varies according to the stage of development reached by the individual, the length becoming proportionately greater with increase in size, as shown by the accompanying data :

Specimen Number	Cephalic Breadth (mm.)	Length/Breadth (as %)
In. 50688	7·0	37
In. 49317	7·5	40
In. 50518	10·0	40
In. 52844	13·5	41
In. 50517	17·0	41
In. 42080	22·0	45

Certain exceptions to this generalization are known, but most, and perhaps all, of them are due to crushing.

The glabella is slightly clavate anteriorly and, in immature individuals, usually carries a median ocellus which is absent from the largest specimens. Glabellar furrows may often be found represented by two pairs of shallow ovoid impressions situated just inwards from the moderately deep axial furrows in the posterior half of the glabella. Hypostomal pits are poorly developed. Each cheek lobe is about as wide as long in the adult, and only moderately convex ; in young individuals the surface is coarsely reticulate, but is smooth by the time the adult stage is reached.

A shallow occipital furrow which deepens laterally demarcates the occipital ring which is produced into a small occipital spine directed backwards and upwards.

The fringe is gently declined frontally and laterally when uncrushed, the surface of the upper lamella being flat, and the pits are often polygonal rather than circular in form, especially at and near the genal flange. The concentric rows E_{1-2} and I_{1-3} are continuous in front of the glabella, and I_4 is almost continuous, extending as far forwards as R3 or R4. The pits of I_{1-3}, especially I_{2-3}, are larger than those of neighbouring rows. The most conspicuous features of *Reuscholithus reuschi* are the complexity and irregularity of the pitting of the fringe, making the application of the usual notation impracticable. Usually the radial arrangement is particularly persistent in I_{1-5}, but beyond a point which may vary from R19 to R22 the pits form a more or less random complex. At and near the anterolateral angles only E_1 occurs outside the girder, though usually with several auxiliary pits, but in front of the glabella pits of E_2 extend as far as R10 or R11, and often there are several adventitious pits situated so as to form a quincuncial pattern with those of E_1 and E_2. Towards the genal angles E_2 is often represented only by occasional adventitious pits, and in the same portion of the fringe E_1 contains numerous small pits, but in some immature individuals E_2 is fairly well developed to the extent of seven or more pits. The holotype (Pl. 14, figs. 1, 3) is one of the largest-known individuals and differs from the more typical forms of the species in the small outward displacement of the pits of E_2, which may occasionally form twin-pits with those of E_1. In the same specimen E_1 contains numerous small pits, only a few of which fall out of line towards the genal angle, so that it is difficult to distinguish any representative of E_2 in that region. The pleuroccipital furrow and segment are transversely straight, but beyond the fulcral sockets the posterior margins of the fringe are convex and extend rearwards to form well-marked " ears ", a feature best shown in the adult trilobite. The holotype has an estimated twelve small pits along the posterior margin of the fringe. Although Bancroft (1929*a* : 83) described the girder as ill-defined, in fact the underside of the fringe carries a usually well-defined girder which becomes stronger medially (see Pl. 14, fig. 9). In young individuals the position of the girder is marked on the upper lamella of the fringe by a smooth concentric " band ", but such a feature is not found in the adult. The fringe perimeter has a small, narrow, raised marginal band and there is a marginal suture of typical trinucleid type. The lower lamella of the fringe is produced posterolaterally into grooved genal spines which curve gently outwards and then inwards. No adult *R. reuschi* has yet been found with the spines entire, but in some immature individuals they are known to extend well beyond the tip of the pygidium.

The thorax consists of six segments of normal trinucleid type, the first macropleural, with the axis occupying about one-fifth of the total breadth. Each axial ring is curved forwards both medially and laterally, and carries a pair of apodemes. The pleurae are flat, each with a broad (*exsag.*), shallow furrow which commences near the anterior margin at the axial furrow and runs outwards and backwards to the blunt, backwardly-directed pleural point. In the case of one specimen (Pl. 14, fig. 4) the faint reticulation just discernible on parts of the cephalon is also found, though still further diminished, on the pleurae.

The pygidium is semi-elliptical in outline, its breadth about four times the length, with a steeply-declined border and a small, raised marginal rim inside of which runs a parallel, broad (*exsag.*), shallow sulcus, giving the pleural lobes a slightly swollen appearance. The axis is small, about one-sixth of the total breadth ; it tapers sharply rearwards and attains the posterior margin. There are two axial rings, and faint suggestions of others. Each pleural lobe carries six pleural furrows which diminish in strength both posteriorly and laterally ; the first two or three pleurae have faintly-marked rib furrows.

IMMATURE INDIVIDUALS. In his original description of the species Bancroft (1929*a* : 83) drew attention to the number of immature specimens found in the *Reuscholithus reuschi* Zone of Coundmoor Brook but as most of these are disarticulated fragments it has not proved possible to work out the ontogeny satisfactorily, though the development of the cephalon is fairly well known.

The smallest specimen (Pl. 14, fig. 11), possibly that referred to by Bancroft (1929*a* : 83), is a poorly-preserved cephalon with two attached thoracic segments. The fringe is incompletely preserved, but shows three concentric rows of pits with a strong radial arrangement ; the breadth is just less than 2·5 mm. and the length about 0·8 mm. This specimen possesses also a pair of occipital pits and two pairs of deep glabellar furrows.

Perhaps the most conspicuous feature of the cephalon of *R. reuschi* is the manner in which the posterior margin of the fringe in immature individuals projects backwards slightly at the fulcral sockets and then, beyond them, curves forwards towards the genal angles which, at their farthest forward position, are situated just behind the line of the median ocellus on the glabella. As development proceeds, the position of the genal angles moves progressively rearwards until in the adult they are situated behind the line of the pleuroccipital furrow, at the tips of the " ears " already mentioned.

All the smallest specimens available possess cheeks and, to a lesser extent, glabella with a coarsely reticulate surface, a median ocellus on the glabella, long alar lobes diverging slightly forwards (see Pl. 14, figs. 6, 10), and well-defined ocular ridges. The last-named join the sides of the glabella approximately in line with the median ocellus, then are directed outwards and slightly backwards to extend through, and a short distance beyond, the axial furrows, and finally terminate in small ocelli. The smallest known specimen, mentioned above, shows traces of branching nervures extending laterally across the cheeks from the ocelli almost to the fringe. During subsequent growth the ocular ridges and ocelli disappear, and in specimens of Meraspis Degree 5 (Pl. 14, fig. 10) with a cephalic breadth of about 5 mm. they are absent, though alar lobes are still well developed. In his description of *Reuscholithus reuschi* Bancroft (1929*a* : 85, text-figs. 4*a*, *b*) gave diagrams purporting to show the early developmental stages, but in his figures the ocular ridges are too long (*tr.*) and the alar lobes are too short and round, lacking the elongate form actually found. One cephalon 7 mm. broad (Pl. 14, fig. 12), probably a young Holaspis, shows neither ocular ridges and ocelli nor alar lobes, but the cheek-lobes retain their coarse reticulation and the glabella its median ocellus. Traces only of fine reticulation have been found in a presumed holaspid cephalon 11 mm. wide (Pl. 14, fig. 4), and the largest known cephalon with a median ocellus is about 16 mm. (estimated) wide (Pl. 14, fig. 7). In common with certain other Trinucleidae the pattern of pit-arrangement appears to have become stable very early during ontogeny, development proceeding mainly by the addition of pits to rows already established. Bancroft's observations (1929*a* : 84) that E_1 and E_2 were formed early, and that subsequent development was essentially the addition of pits to the region internal to the girder, appear to be correct.

Horizon and localities. The holotype was collected from the old cartway near the south-eastern corner of Smeathen Wood, Horderley, where the species occurs uncommonly in yellow, sandy mudstones, the Smeathen Wood Beds, associated with *Smeathenia smeathenensis* (Bancroft), *Phacopidina harnagensis* Bancroft, *Salopia salteri* (Davidson) and *Smeathenella harnagensis* Bancroft. In the Cressage District the principal localities are in Coundmoor Brook, *a.* by the north bank about 1300 yards south-west of Harnage Farm, *b.* by the north bank 1310 yards south-west of Harnage Farm, and *c.* in the south bank about 85 yards east-north-east of the north-eastern end of the large disused quarry near Stevenshill, but the species may be expected to be found at numerous other places in the vicinity where the Harnage Shales crop out, particularly in Coundmoor Brook immediately west of Coundmoor itself. Elsewhere *R. reuschi* has been found at localities along the small stream running between Gutter Cottage and Wallsbank Farm, east-north-east of Hope Bowdler. Owing to the unsuitability of the environment no larval forms have been found at the type-locality, and all such specimens described are from the Cressage and Wallsbank districts.

Holotype. BM. In. 42080 *a, b*. An incomplete cephalon first figured by Bancroft (1929*a* : pl. 1, fig. 3) and here refigured (Pl. 14, figs. 1, 3).

Paratypes. The pygidium figured by Bancroft (1929*a* : pl. 1, fig. 4) has not yet been found, and it has not proved possible to trace with certainty the original of his schematic diagrams (1929*a* : pl. 1, figs. 5*a, b*).

Other specimens. BM. In. 50688 (Pl. 14, fig. 2); BM. In. 51501 (Pl. 14, fig. 4); BM. In. 50671 (Pl. 14, fig. 5); BM. In. 54028 (Pl. 14, fig. 6); BM. In. 50517 (Pl. 14, fig. 7); BM. In. 50519 (Pl. 14, fig. 8); BM. In. 49316 (Pl. 14, fig. 9); BM. In. 50665 (Pl. 14, fig. 10); BM. In. 50667 (Pl. 14, fig. 11); BM. In. 49317 (Pl. 14, fig. 12); BM. In. 50668 (Pl. 14, fig. 13); BM. In. 50672 (Pl. 14, fig. 14).

Discussion. The irregular nature of the pitting of the fringe of *Reuscholithus reuschi* makes it unlikely to be confused with any other trinucleid. Bancroft (1935 : 333) derived *Reuscholithus* from *Marrolithus*, and it now appears highly likely that in *Costonia* we have a transition, both morphological and stratigraphical, between the two genera. *R. reuschi* bears a particularly noticeable resemblance to *Costonia elegans*, but may easily be distinguished by the total absence of inflated pits in E_1, by the development of E_2 both anteriorly and pósterolaterally, and by the much more random distribution of pits generally. Nothing else comparable with *R. reuschi* is known, and Størmer's inclusion (1930 : 40) of the Shropshire species in the synonymy of what he called *Cryptolithus dicors* [*sic*] Angelin sp., a form which probably belongs to *Broeggerolithus*, is certainly incorrect.

Genus ***SALTEROLITHUS*** Bancroft, 1929

The generic name *Edgellia* was proposed by Shaw (*in* Shaw & Stubblefield, 1950 : 624) for *Trinucleus fimbriatus* Murchison, 1839, in the belief that the type-species of *Trinucleus* was *T. caractaci*. However, as Vogdes (1890 : 84) had already selected *T. fimbriatus* as the type-species of *Trinucleus*, *Edgellia* became an objective synonym of *Trinucleus* thus leaving *Salterolithus* Bancroft unaffected and available for use. *Salterolithus caractaci* has already been described in detail by both Cave (1957) and Whittard (1958) but, as the latter author has pointed out, Bancroft has at various times assigned to the genus trilobites with fringes which differ markedly from that of the type-species. These are listed below, together with the writer's interpretation of them.

a. *Salterolithus harnagensis* Bancroft (1929*a* : 79, pl. 1, fig. 1), from the basal Harnagian Stage of the Cressage district. No pits external to E_2. Similarly *Salterolithus* aff. *harnagensis* Bancroft from the basal Harnagian deposits forming Neptunian dykes at Hazler Hill, east of Church Stretton (Bancroft, 1949 : 291, pl. 10, fig. 15).

b. *Salterolithus harnagensis* Bancroft var. from " immediately above the Hoar Edge Grits " (Bancroft, 1929*a* : 80). Incipient E_3 developed by the division of E_2.

c. *Salterolithus* sp. E_3 well developed. Said to be an associate of *Salterolithus harnagensis*, and particularly characteristic of an horizon which Bancroft (1929*a* : 81) described as existing " between the *S. harnagensis* and *Reuscholithus reuschi* Zones ".

d. *Salterolithus* cf. *intermedius* (Wade) from " the lower 30 feet of the Harnage Shales at Horderley " (Bancroft, 1929*a* : 82). E_{3-4} well developed.

e. *Salterolithus smeathenensis* Bancroft (1949 : 292, pl. 9, figs. 1, 2, 2*a*) from the basal Harnagian near Horderley. E_{3-4} well developed, small development of E_5.

A reference by Bancroft (1949 : 293) to E_5 in a later description of *Salterolithus caractaci* is thought by Whittard (1958 : 84) to be possibly a misprint. Of the fringe-types listed above, that of group *a*. is, as suggested by Whittard (1958 : 83), probably best included in the genus *Broeggerolithus*, though this is a broad interpretation. The so-called *Salterolithus harnagensis* lacks certain features of the typical species of *Broeggerolithus*, and can probably be regarded as a primitive member of the genus. The form listed above in group *b*. has not yet been traced with certainty, but may also belong to *Broeggerolithus* (*s.l.*).

The *Salterolithus* sp. of group *c*. is thought to be a true member of the genus, and is almost certainly that described in the present paper as *Salterolithus praecursor* sp. nov. The species in group *d*. is without doubt the same as that described later as *Salterolithus smeathenensis* Bancroft, a species which comprises also group *e*. and is made the type of a new genus *Smeathenia* elsewhere in this paper.

DISTRIBUTION. In south Shropshire the first known occurrence of *Salterolithus* (*s.s.*) is in the shales and mudstones of the *Reuscholithus reuschi* Zone at Coundmoor Brook, near Cressage, just above the basal sandy beds of the Harnagian Stage. In the south of the Caradoc Area the genus does not appear until slightly later, in the *Salterolithus caractaci* Zone of the Harnagian. No definite records exist for the

Broeggerolithus ulrichi Zone, though this is likely to be due to the general paucity of fossils at the horizon rather than to actual absence, for *Salterolithus caractaci* itself is found, though not commonly, in the Lower Soudleyan, the last-known occurrence of both genus and species.

These records of *Salterolithus* in south Shropshire correspond in a general way with the limits of the *Diplograptus multidens* Zone as now interpreted there. Outside the Caradoc Area the genus occurs in the Soudleyan of the Pontesford District, the Harnagian and Soudleyan of the Shelve Inlier, the Harnagian of the Welshpool District, and is also known from the Breidden Hills, the Bala District, and the Dinas Mawddwy District of Merioneth (Pugh, 1928 : 351).

TYPE-SPECIES. *Trinucleus caractaci* Murchison, 1839 by original designation of Bancroft (1929*a* : 78).

Salterolithus caractaci (Murchison)

(Pl. 15, figs. 1, 2, 4, 6 and 9)

1839. *Trinucleus caractaci* Murchison, pp. 303, 650, 659, pl. 23, figs. 1*a–c* only.
1853. *Trinucleus concentricus* (Eaton) : Salter, pp. 3, 5.
1854. *Trinucleus concentricus* (Eaton) : Murchison, p. 203, pl. 4, figs. 2, 4, 5.
1859. *Trinucleus concentricus* (Eaton) : Murchison, p. 224, pl. 4, figs. 2, 4, 5.
1867. *Trinucleus concentricus* (Eaton) : Murchison, p. 204, pl. 4, figs. 2, 4, 5.
1872. *Trinucleus concentricus* (Eaton) : Murchison, p. 204, pl. 4, figs. 2, 4, 5.
1911. *Trinucleus intermedius* Wade, pp. 449–50, pl. 36, figs. 1, 2.
1911. *Trinucleus concentricus* var. *caractaci* Murchison, Wade, p. 424.
1913. *Trinucleus caractaci* Murchison : Raymond, p. 4.
1913*a*. *Cryptolithus caractaci* (Murchison) Raymond, pp. 28, 30.
1927. *Cryptolithus caractaci* (Murchison) : Stetson, pp. 89, 95.
1928. *Trinucleus caractaci* (Murchison) : Pugh, pp. 351–353, 375, 379.
1929*a*. *Salterolithus caractaci* (Murchison) Bancroft, pp. 74, 78, 82.
1933. *Salterolithus caractaci* (Murchison) : Bancroft, table 3.
1941. *Salterolithus caractaci* (Murchison) : Whittington, p. 25.
1949. *Salterolithus caractaci* (Murchison) : Bancroft, pp. 293–4.
1950. *Trinucleus caractaci* Murchison : Shaw & Stubblefield, p. 624.
1957. *Salterolithus caractaci* (Murchison) : Cave, p. 284, pl. 10, figs. 3–6.
1958. *Salterolithus caractaci* (Murchison) : Whittard, p. 85, pl. 12, figs. 2–6.
1958. *Salterolithus caractaci* (Murchison) : Dean, p. 201, pl. 26, fig. 5.
1958. *Salterolithus* sp. nov., Dean, p. 203.

The species was erected by Murchison (1839 : 659, pl. 23, figs. 1*a–f*) using six syntypes, four of which were figured and all of which he claimed were from " a little dingle west of Welch Pool Church ", a place known to geologists as " Trilobite Dingle ". These specimens are in the Geological Society Collection at the Geological Survey and Museum, and are numbered 6828–6832, 6834. Of the syntypes, 6828, 6833 and 6834 are labelled as being from Welshpool, and 6830 forms part of a block of grey mudstone from Wistanstow, written as Wistantow [*sic*]. The remaining specimen 6829 is not labelled, but according to the original register it, too, is from Wistanstow. Recently Cave (1957 : 284) has selected as lectotype specimen 6829 on the grounds that it agrees best with the mode of the population as established by him on a statistical basis for *S. caractaci* in the Welshpool district, and that it agrees lithologically with material from Trilobite Dingle (Bron-y-Buckley Wood), Welshpool. Whittard has expressed concern at this choice of lectotype (1958 : 83) owing to the apparent doubt regarding the original locality and the colour of the matrix, and would have preferred to choose specimen 6834, which is undoubtedly from Welshpool. The writer feels that these doubts are needless as Cave's lectotype agrees best with known Welshpool material from Trilobite Dingle ; it is certainly not from the Wistanstow district as stated in the Geological Survey register, and it seems likely that a mistake occurred in the original registration. The adjacent numbers refer to specimens which do, in fact, derive from near Wistanstow, and specimens 6830–6832, all on the same hand-specimen, are typical *Onnia superba* (Bancroft) from the Onny Valley. *Salterolithus caractaci* occurs in the middle Harnagian and Lower Soudleyan of the Onny Valley near Horderley, but there is no resemblance between the lithologies there and at Welshpool.

It is not proposed to describe *Salterolithus caractaci* in detail here in view of the very complete descriptions already available and noted above. Cave (1957 : 285) has given the following data for the outermost rows of fringe-pits : external to $E_1 = 35$–79, mode $= 58$; $E_1 = 26$–29, mode $= 27$; $I_1 = 23$–28, mode $= 25$ or 26. The specimens from the Harnagian of south Shropshire figured in this paper (Pl. 15, figs. 1, 2) have the following numbers of pits : external to $E_1 =$ about 58 ; $E_1 + e_1 = 26$; $I_1 + i_1 = 26$, and can thus be seen to conform extremely closely to the average member of the Welshpool population. Of the specimens collected from the Lower Soudleyan of the Onny Valley and assigned to *S. caractaci*, a typical individual, In. 51207, has the following pit-count : external to $E_1 = 59$; $E_1 + e_1 = 28$; $I_1 + i_1 = 28$; $I_2 + i_2 = 26$. This is once again very close to the mode of the Harnagian population described from Welshpool, and there can be no doubt of the identity of the two forms.

HORIZONS AND LOCALITIES. Bancroft (1949 : 294) recorded *Salterolithus caractaci* from two closely adjacent excavations, localized as being 700 feet due north of Glenburrell Farm, Horderley, from which abundant specimens were collected, and it was partly upon these discoveries that he founded the *Salterolithus caractaci* Zone of the Harnagian Stage. *S. caractaci* has also been found, at apparently the same horizon, about 90 yards south-east of the eastern end of the large disused quarry in Hoar Edge Grits by the south-western bank of the River Onny south-west of Round House, Horderley. Elsewhere in the Harnagian of the Caradoc Area, fragmentary evidence suggests that the species may occur in the stream-section just east of Gutter Cottage, east-north-east of Hope Bowdler.

Bancroft wrote (1949 : 294) " at the horizon of the *Horderleyella* burst at Horderley there is a form in which I_3 seems to extend farther anteriorly than in *Salterolithus caractaci* forma typica ". The horizon of the so-called " *Horderleyella* burst " is now believed to form part of the *Broeggerolithus broeggeri* Zone of the Soudleyan Stage. The species in question is probably that listed subsequently as *Salterolithus* sp. nov. (Dean, 1958 : 203), and figured here (Pl. 15, figs. 4, 9) as *S. caractaci* from the stream-section at the extreme north-eastern corner of Smeathen Wood, near Horderley. At the time the former identification was made it appeared that the species might be new, but additional specimens, together with the detailed descriptions of *S. caractaci* by Cave and Whittard, have shown that the Soudleyan form falls within the limits of variation of *S. caractaci* itself. The species occurring in the Soudleyan of Pontesford Brook, near Pontesbury (Dean, 1958 : 228), is apparently the same as that from Smeathen Wood.

In the Shelve Inlier *Salterolithus caractaci* is recorded from near the top of the Aldress Shales, from the Hagley Shales, and from the Whittery Shales, all of which horizons are included in the *Broeggerolithus broeggeri* Zone of the Soudleyan (Whittard, 1958 : 86–87). These strata are also equated with part of the *Diplograptus multidens* Zone (Whittard, 1956 : 5), thus affording some confirmation of the correlation of shelly and graptolitic faunas proposed for south Shropshire (Dean, 1958 : 227).

FIGURED SPECIMENS. BM. In. 51339 (Pl. 15, fig. 1) ; BM. In. 51340 (Pl. 15, fig. 2) ; both from the Harnagian Stage. BM. In. 51205 (Pl. 15, fig. 9) ; BM. In. 51207 (Pl. 15, fig. 4) ; BM. In. 51193 (Pl. 15, fig. 6) ; all from the Lower Soudleyan Stage.

Salterolithus praecursor sp. nov.

(Pl. 15, figs. 3, 5, 7, 8, 10–12)

1929*a*. *Salterolithus* sp., Bancroft, p. 81.

DESCRIPTION. The cephalon is normally moderately convex, both longitudinally and transversely, and sub-semicircular in plan, although anterolaterally it sometimes appears slightly angular when flattened. The length is about, or slightly more than, half the maximum breadth when uncrushed, and the largest-known specimen is 24 mm. wide, excluding genal spines. The glabella is tumid, slightly expanded anteriorly, about twice as long as broad, separated from the plump, quadrant-shaped cheek-lobes by broad, moderately-deep axial furrows which are slightly convex outwards. There is a poorly-defined occipital furrow and the occipital ring is produced to form a small spine directed backwards and upwards. The pleuroccipital segment is small, extending only halfway from the axial furrow towards the lateral margin, and is separated from the cheek-lobes by a pleuroccipital furrow which becomes shallower and broader (*exsag.*) outwards. The fringe has a flat upper surface and is only moderately declined anteriorly and laterally. It is relatively broad (*exsag.*), about one quarter to one third of the cephalic length, and of fairly uniform width almost as far as the posterolateral borders which are produced backwards to form small " ears " terminating laterally in stout genal spines, each of which is curved outwards and backwards and carries a longitudinal median ridge on the underside. There are five concentric rows of fringe-pits which are complete or nearly so, E_{1-3} and I_{1-2}, and of these E_1 and I_{1-2} comprise pits of approximately uniform size, slightly larger than those of adjacent rows. At the median line the rows I_{1-2} are flexed forwards slightly so as to accommodate the front of the glabella. There is a marked concentric arrangement of pits, with a slightly less marked radial arrangement. E_{1-3} are grouped closely together, but well-defined concentric bands occur between E_1–I_1, and between I_1–I_2 ; the first of these corresponds in position with a well-developed girder, bearing longitudinal striae, on the lower lamella of the fringe, and the second with a pseudogirder which is only developed laterally and posterolaterally. As one might expect, the number of fringe pits varies, particularly with the size of the individual trilobite, and the number present in rows E_{2-3} ranges from about 35 in a cephalon 7 mm. wide to 54 in one 24 mm. wide. For the principal rows of pits the number present is $E_1 + e_1 = 21\text{–}25$ (variation), 22 (mode) ; $E_{2-3} + e_{2-3} = 43\text{–}54$ (variation), 49 (mode) ; $I_1 + i_1 = 19\text{–}23$ (variation), 22 (mode) ; insufficient material has been found with I_2 intact, but in the holotype this row contains 21 pits. Auxiliary pits are commonest in the anterior and lateral portions of the fringe, where they are almost confined to E_{2-3}, those of E_3 being sometimes slightly displaced outwards.

The thorax and pygidium are not known from the type-locality, but an immature whole individual which probably belongs to the species is figured here from the Wallsbank district (Pl. 5, fig. 12). The thorax is of normal trinucleid type, with six segments and an axis occupying just less than one quarter of the total breadth. The pygidium, preserved as an internal mould, is subtriangular in outline, bluntly-pointed posteriorly, and the axis, which carries at least three small axial rings, is weakly defined, grading into the side-lobes where there are only two pleurae visible.

Horizon and localities. The holotype, together with the paratypes In. 52031 and In. 52036, is from the south side of Coundmoor Brook, about 20 feet above stream level and 1340 yards south-west of Harnage Farm. The other paratype, In. 52017 is from the bed of Coundmoor Brook by the north bank, about 1320 yards south-west of Harnage Farm, In. 52041 from the south bank of Coundmoor Brook 1356 yards south-west of Harnage Farm, and the whole individual In. 54027 from the south bank of The Gutter, 450 yards east-south-east of Gutter Cottage, near Wallsbank. All these occurrences are in grey shales and mudstones, the Harnage Shales (*s.s.*), belonging to the *Reuscholithus reuschi* Zone of the Harnagian Stage.

In a recent paper (Dean, 1958 : 201) it was suggested that the base of the Harnagian Stage in the Cressage district should be defined by the appearance of *Reuscholithus* and/or *Salterolithus*. The *Salterolithus* in question was not *S. praecursor* sp. nov., but *Broeggerolithus harnagensis* (Bancroft), a species which was at that time referred to *Salterolithus*. *Salterolithus praecursor* has not yet been discovered with certainty outside the Cressage district, where it occurs only uncommonly.

Holotype. BM. In. 51479 (Pl. 15, fig. 3).

Paratypes. BM. In. 50517 (Pl. 15, fig. 10) ; BM. In. 52031 (Pl. 15, fig. 5) ; BM. In. 52036 (Pl. 15, fig. 5).

Other figured specimens. BM. In. 51840 (Pl. 15, fig. 7) ; BM. In. 52041 (Pl. 15, fig. 8) ; BM. In. 54027 (Pl. 15, fig. 12).

Discussion. The only trinucleid trilobite which might usefully be compared with *Salterolithus praecursor* sp. nov. is *S. caractaci* (Murchison), discussed elsewhere in this paper, and confusion is unlikely as there are several differences between the two. Generally speaking *S. praecursor* is a much smaller species than *S. caractaci*, and the largest-known specimen is only 24 mm. wide across the base of the cephalon, compared with a width of 30 to 40 mm. which is not uncommon in the latter species. The cephalon of *S. praecursor* is also more rounded in outline and convex in form, though this is often obscured by its occurrence, with resultant crushing, in shaly mudstones. On the upper lamella of the fringe of *S. praecursor* the smooth concentric "bands" situated between E_{1-2} and between I_{1-2} are much narrower (*exsag.*) and less conspicuous than in *S. caractaci*, and the pit count for all the principal rows is noticeably less.

Genus ***SMEATHENIA*** nov.

DIAGNOSIS. Cephalon moderately convex both laterally and transversely, outline strongly and evenly curved, with the genal angles produced backwards to form large "ears". Cephalic fringe broad, maintaining its breadth evenly around the entire border. I_{1-2} continuous in front of the glabella. E_{1-3} extend to the genal angle, E_4 just fails to reach it, and E_5 is represented by adventitious pits in E_4 which may extend as far as R14. I_{1-2} and E_1 are composed of large pits, those of E_2 are slightly smaller, whilst those of E_{3-5} are noticeably smaller still. Thorax made up of six segments of typical trinucleid type, with narrow axis. Pygidium subtriangular in outline, usually with four or five axial rings, and two or three poorly-defined pleurae on the slightly inflated pleural lobes.

DISTRIBUTION. *Smeathenia* is known only from the southern portion of the Caradoc District of south Shropshire, where it is characteristic of the *Reuscholithus reuschi* Zone of the Harnagian Stage. It is broadly contemporaneous with *Broeggerolithus harnagensis* (Bancroft), but as yet the two have been found neither together nor in the same succession.

DISCUSSION. The new genus differs markedly from *Salterolithus*, to which the type-species has previously been referred, in possessing a well-developed E_4 together with a poorly-developed E_5.

TYPE-SPECIES. *Salterolithus smeathenensis* Bancroft, 1949.

Smeathenia smeathenensis (Bancroft)

(Pl. 13, figs. 7, 10–16)

1929*a*. *Salterolithus* cf. *intermedius* (Wade) Bancroft, p. 82.
1949. *Salterolithus smeathenensis* Bancroft, p. 292, pl. 9, figs. 1, 2, 2*a*.
1958. *"Salterolithus" smeathenensis* Bancroft: Whittard, p. 84.
1958. *Salterolithus smeathenensis* Bancroft: Dean, p. 201, pl. 26, fig. 4.

DESCRIPTION. Cephalon wider than long, with outline well rounded forming more than half an ellipse, the genal angles being produced backwards to form moderately large "ears". In the lectotype the length, including the "ears" and excluding the genal spines, is 12·5 mm. and the breadth 19 mm., but this specimen is slightly flattened. In occasional uncrushed specimens the maximum breadth is across the line of the pleuroccipital furrows, with the lateral margins converging backwards slightly towards the genal angles. The glabella is strongly convex longitudinally, slightly clavate in outline, usually with a poorly-defined median ocellus. Basal glabellar furrows are represented by one pair of small, deep, circular pits situated a short distance in front of the shallow occipital furrow which contains a pair of deep occipital pits slightly larger in size than those of the glabellar furrows.

The occipital ring is small, produced into a short occipital spine, directed backwards and upwards. The cheek-lobes are quadrant-shaped, moderately inflated, and smooth in the adult ; in the young form they carry coarse reticulation which becomes finer towards the inner margin of the fringe. Separating the cheek-lobes from the glabella are broad, shallow axial furrows with small, deep hypostomal pits sited well forward, close to the fringe. Near to the intersection of each axial furrow and the occipital ring there is a conspicuous pit situated to the rear of centre of each of the narrow (*exsag.*) pleuroccipital segments. The last-named are transversely straight as far as the fulcral sockets, beyond which the posterior margins of the fringe run outwards and backwards to the genal spines which are splayed outwards, each with a median groove. The border of the fringe is steeply declined, carrying, near the top, the marginal suture, separated from the pits of the upper lamella by a narrow marginal band. At the genal angle the line of the marginal suture skirts the pitted area and turns through more than a right angle so as to run parallel to, and then cut, the posterior margin of the fringe just before reaching its mid-point, finally disappearing below the underside of the cephalon. Possessing as it does a large number of concentric rows of pits, the fringe appears very broad (*exsag.*), particularly in flattened specimens, and maintains this breadth in front of the glabella. I_{1-2} and E_1 are continuous, both in front of the glabella and as far as the posterior margin of the fringe and genal angle ; they consist of pits which are larger than those of adjacent rows, and increase slightly in size towards the genal angles. I_1 and E_1 are separated on the upper lamella by a smooth, and occasionally slightly raised, concentric band which corresponds in position with the girder on the underside of the lower lamella. There is some diminution in the size of pits outwards from E_1. A strong radial arrangement is found only in I_{1-2} and E_1 where it extends to within two or three pits of the posterior fringe-margin, usually as far as R20 or R21. It has not proved practicable to use the usual notation for the rows of pits external to E_1. Although the frontal portion of the fringe lacks any satisfactory radial arrangement other than in I_{1-2} and E_1, from about R9 or R10 to R14 radial rows can be traced beyond E_1 where they curve outwards and backwards to the margin. In the lectotype E_2 has 27 pits and extends to the genal angle, E_3 has 30 pits and extends almost as far as E_2, E_4 and E_5 include numerous small pits several of which may be arranged in a random manner or so as to form a quincuncial pattern, E_5 extending as far as R14. It is frequently difficult, in the case of trinucleid genera such as *Salterolithus* and *Smeathenia*, to give adequate notational representation of the pits in the outermost concentric rows, and more recently Cave (1957) has found it convenient to work out the mode for both E_1 and the number of pits external to E_1 in *Salterolithus caractaci*. Such a procedure is particularly useful for *Smeathenia smeathenensis*, in which species the number of pits external to the girder may vary from 90 to 120, the number depending to some extent on the size of the individual. The fringe of the lectotype, a large cephalon 19 mm. wide, contains 95 pits external to E_1, but the corresponding number in a cephalon 14 mm. wide is only 73.

The thorax is made up of six segments of normal trinucleid type, and the greatest breadth is across the third, fourth and fifth segments, which are of equal size. The thoracic outline narrows forwards noticeably to the macropleural first thoracic segment. The side-lobes are flat and the axis moderately convex, occupying rather more than one-quarter of the total breadth. Each axial ring carries a deep articulating furrow in which is situated a pair of deep apodemal pits, and each pleura is divided into two pleural bands, of which the posterior band is the broader (*exsag.*), by a shallow pleural furrow which commences at the axial furrow and runs outwards and slightly backwards to the blunt, backwardly-directed, pleural point.

The pygidium is about three times as long as broad, its outline almost semi-elliptical or very slightly angular posteriorly and posterolaterally. The axis is between one-quarter and one-fifth of the total breadth, and is bounded by poorly-defined axial furrows ; there are four or five axial rings on the external mould, diminishing posteriorly, but the number on the internal mould is smaller, and of these the first two possess pairs of apodemal pits. The marginal parts of the pleural lobes are somewhat tumid both laterally and posteriorly, and there are usually two pairs of pleural furrows which deepen slightly towards the lateral margins. There is a gently convex postaxial ridge extending from the axis to the posterior margin, where a small blunt projection is usually developed.

HORIZON AND LOCALITIES. The type-locality is the section in the small cutting or cartway near the south-eastern corner of Smeathen Wood, 250 yards west-south-west of Wood House, five-sixths of a mile south of Horderley Station, where *S. smeathenensis* occurs in the lower part of the Smeathen Wood Beds associated with *Reuscholithus reuschi* Bancroft, *Phacopidina harnagensis* Bancroft and *Smeathenella harnagensis* Bancroft. The species is also abundant at the field exposure 550 yards north-west of Woolston House, Woolston, in a more arenaceous development of the Smeathen Wood Beds. All specimens known are from the *Reuscholithus reuschi* Zone of the Harnagian Stage in the general area of the River Onny Valley, and the species has not yet been found elsewhere.

LECTOTYPE, here selected. BM. In. 43321 (Pl. 13, fig. 16), the cephalon figured by Bancroft (1949, pl. 9, fig. 1).

PARATYPES. BM. In. 42082, an incomplete cephalon figured by Bancroft (1949, pl. 9, fig. 2) ; BM. In. 42092 (Pl. 13, fig. 15), the external mould of a pygidium figured by Bancroft (1949, pl. 9, fig. 2*a*) as a gutta-percha cast.

FIGURED SPECIMENS. BM. In. 49132 (Pl. 13, fig. 7) ; BM. In. 49560 (Pl. 13, figs. 10–12) ; BM. In. 50619 (Pl. 13, fig. 13) ; BM. In. 50767 (Pl. 13, fig. 14).

DISCUSSION. *Smeathenia smeathenensis*, the only species of the genus yet known, is easily distinguished from superficially similar trinucleids, for example *Salterolithus*, by the strong development of E_4 and the weak development of E_5.

Genus ***BROEGGEROLITHUS*** Lamont, 1935 *ex* Bancroft MS.

1933. *Broeggeria* Bancroft, p. 2. Preoccupied by *Broeggeria* Walcott, 1903.
1933. *Ulricholithus* Bancroft, p. 2. *Nomen nudum.*
1949. *Salterolithus* (*Ulricholithus*) Bancroft, p. 295.

The type-species of *Broeggerolithus* has been described by Bancroft (1929*a* : 85, pl. 1, figs. 6–8) and, more recently, by Whittard (1958 : 89, pl. 12, figs. 7–13). In diagnosing the genus the latter author has advocated (1958 : 88) that " forms with adventitious pits of an incipient E_3 series should be excluded from *Broeggerolithus* ". He has also expressed doubt as to whether *Broeggerolithus* and *Onnia* should be maintained as separate genera, but this view is not supported here (see p. 127). The genus *Broeggerolithus* covers a large and variable group of Trinucleidae, ranging through a considerable proportion of the Caradoc Series. Interpreted in a broad sense, it can be divided on the basis of fringe form into three groups of species as follows.

Group 1. Typified by *B. harnagensis* (Bancroft). Cephalic outline conspicuously rounded, almost semicircular, much shorter than broad. Coarse reticulation of the cheek-lobes may occur in the adult as well as the young forms. E_{1-2} and I_{1-2} are virtually complete, a few pits of E_2 being absent at the genal angle ; the pits of the four outermost rows are usually almost circular in form and of fairly uniform size. The upper lamella of the fringe is smooth, and there is no development of interradial or concentric ridges. E_2, and, to a much lesser degree, that part of the fringe between E_1 and E_2, contains several auxiliary pits, often irregularly disposed, though there is no suggestion of the development of an incipient E_3. The group is known only from the lowest Harnagian Stage in south Shropshire, and probably occurs at about the same horizon, or perhaps slightly earlier, in North Wales. Only one species has so far been described.

Group 2. Cephalon generally noticeably shorter than broad, with subangular outline. E_{1-2} and I_{1-2} usually complete, though up to a total of 8 pits may be absent from E_2 frontally, and up to 5 pits of E_1 are external at the genal angle owing to the incomplete development of E_2 there. Interradial ridges are generally strongly developed, particularly at E_1 which contains larger pits than, and is elevated above, adjacent concentric rows. Geological range is from the topmost Harnagian Stage to the Upper Longvillian Substage, and species, in stratigraphical order, include *ulrichi*, *broeggeri*, *constrictus*, *soudleyensis*, *globiceps* and, doubtfully, *simplex*. *B. ulrichi* differs in certain respects from the general plan outlined above, for example the cephalon is longer and more rounded, and there are several auxiliary pits in front of the glabella, a feature not usually found, but these differences are outweighed by the similarities. In any case, what is possibly the earliest member of the group might be expected to exhibit certain atypical or transitional characters.

Group 3. The third group of species of *Broeggerolithus* (*s.l.*) has not been distinguished by a separate subgeneric name, but this may eventually prove necessary when the various forms are better understood. So far only two species, *longiceps* and *transiens*, are definitely involved, ranging from the base of the Upper Longvillian Substage to the end of the Marshbrookian Stage in Shropshire. The cephalon has a well-rounded outline and is proportionately longer than in other groups, with a long, high glabella. The cheek-lobes of some specimens retain a reticulate surface even in the adult, but the importance of this is uncertain. There is only a weak development of interradial ridges on the upper lamella of the fringe which is almost flat, no one concentric row being elevated above the rest. E_{1-2} and I_{1-2} are complete or nearly so, even in the case of E_2 at the genal angle, and the size of pit does not vary markedly between the four outermost concentric rows. A few auxiliary pits may occur in E_2 laterally. The lessening development of interradial ridges parallels that in *B. ulrichi*, the earliest-known species of Group 2, and may indicate a retrogressive trend after the close of the Lower Longvillian Substage.

In his first paper dealing with the Trinucleidae Bancroft (1929*a* : table facing p. 76) gave a zonal table of the Caradoc succession and listed the " fringe-type of dominant group " at various horizons throughout the Series ; certain details of these fringe-types were also enumerated in the same work (1929*a* : 73–76). The types of fringe listed by Bancroft are as follows : of them the lowest, *a*, does not concern us here as it is not an Anglo-Welsh form. There is a break in the Table between *g*. and *h*. corresponding with the Actonian Stage, which has not yet yielded identifiable trinucleid trilobites in Shropshire.

h. *superbus* type.
g. modified *gibbifrons* type (without depressed I_1).
f. *gibbifrons* type.
e. *soudleyensis* type (E_2 absent in front).
d. *broeggeri* type (intercalation in E_2 in front).
c. *caractaci* type (E_3 generally represented).
b. *favus* type.
a. *subradiatus* type.

Of these, *a*. is now *Reedolithus*, *b*. covers both *Marrolithus* and *Costonia*, *c*. is *Salterolithus*, *d*.–*g*. include various groups of *Broeggerolithus* (*s.l.*), and *h*. is now *Onnia*. The so-called " *gibbifrons*-type " of fringe is a misnomer and, although the name is widely quoted, is best abandoned. The type-specimens of *Trinucleus gibbifrons* McCoy, 1851 are lost. Williams (1948 : 80), in discussing the species, has shown that only rocks of Llandeilo age occur at the type-locality of Golden Grove, Llandilo, and it is suggested that the name be rejected. It seems more than likely that Bancroft's frequent usage of the term and its eponymous species stems from Reed's description and figure of a so-called *T. gibbifrons* McCoy (Reed, 1914 : 356, pl. 29, fig. 6) from Gelli Grin (probably the Gelli Grin Limestone or Calcareous Ash of Longvillian age) in the Bala District, a form which more closely resembles *Broeggerolithus globiceps* (Bancroft), and belongs apparently to *Broeggerolithus* (*s.s.*).

Distribution. There is some ambiguity as to the stratigraphical level at which Bancroft believed *Broeggerolithus* made its appearance (Whittard, 1958 : 88), but the new collections available show that in south Shropshire *Broeggerolithus* (*s.l.*) appears in the lowest Harnagian and ranges upwards almost without interruption as far as the top of the Marshbrookian. The genus is not yet known with certainty from higher horizons in England or Wales. Geographically it is widespread, occurring also in the Shelve Inlier and at Pontesford, both in west Shropshire, as well as in many parts of North Wales, the Cross Fell Inlier, and the Dry Gill area of the Lake District. In Scandinavia it may possibly be represented by *Trinucleus discors* Angelin, 1854, a species usually placed in *Cryptolithus* but possessing two rows of pits external to the girder. Whittington (1941 : 30–34) refers the American species *Cryptolithus lorrainensis* Ruedemann, 1925, from the Lorraine Formation of New York State, to *C. bellulus* (Ulrich), but Lamont (1941 : 468, pl. 5, fig. 9) tentatively includes a small specimen from the Lorraine Formation of Rome, New York State, in the former species and states that both E_1 and E_2 are present on the fringe. Whether or not Lamont's specimen is the same as *C. lorrainensis* is outside the scope of this paper, but the presence of two rows of pits external to the girder strongly suggests that *Broeggerolithus* may be represented in the North American faunas.

TYPE-SPECIES. *Cryptolithus broeggeri* Bancroft, 1929, by original designation of Bancroft (*in* Lamont, 1935 : 320).

Broeggerolithus harnagensis (Bancroft)

(Pl. 16, figs. 5, 9, 13)

1929*a*. *Salterolithus harnagensis* Bancroft, p. 79, pl. 1, figs. 1, 2.
1933. *Salterolithus harnagensis* Bancroft : Bancroft, table 3.
1949. *Salterolithus harnagensis* Bancroft : Bancroft, p. 291.
1955. *Salterolithus harnagensis* Bancroft : Whittington *in* Whittington & Williams, p. 420.
1956. *Salterolithus harnagensis* Bancroft : Harper, p. 386.
1958. *"Salterolithus" harnagensis* Bancroft : Whittard, p. 83.
1958. *Salterolithus harnagensis* Bancroft : Dean, pp. 200, 201.

DESCRIPTION. The cephalic outline is well rounded, almost semicircular, the maximum breadth being a little more or less than two and a half times the median length, excluding occipital spine. The glabella is clavate, swollen anteriorly, with a small median ocellus and, apparently, does not stand very high above the plump cheek-lobes, from which it is separated by broad, shallow, almost straight, axial furrows containing large, deep, hypostomal pits. The surface of the cheek-lobes of young individuals is almost always coarsely reticulate, but occasionally may be smooth and it is not yet clear whether this is a primary feature or merely an accident of preservation. The front of the glabella intrudes only slightly on to the fringe and I_2, continuous there, is barely flexed forwards in consequence. No undoubted glabellar furrows have been seen, but there is a pair of deep apodemal pits situated just inwards from the axial furrows, immediately in front of the occipital furrow. The latter is broad (*sag.*), shallow, and ends laterally in a pair of deep occipital pits ; it delimits a small occipital ring which is directed upwards and slightly backwards, and produced into a small occipital spine. At the outer ends of the occipital ring are sited a pair of deep pits indenting the posterior margin ; from them the narrow (*exsag.*) pleuroccipital segment and moderately deep pleuroccipital furrow run straight outwards to the fulcral sockets, less than halfway to the lateral margins. From the fulcral sockets the posterior margins of the fringe, slightly convex rearwards, are directed outwards and fairly markedly backwards so as to form large " ears ". The genal spines are imperfectly known, but appear to be smooth on their upper surfaces, longitudinally ridged on the under surfaces, and strongly divergent rearwards. There is a narrow marginal band, truncated by the vertical border, just below the top of which runs the marginal suture, of normal trinucleid type.

The cephalic fringe is moderately broad, uniformly so over most of its length, expanding markedly behind the posterolateral angles of the cheek-lobes. The upper lamella is generally smooth, and no concentric or interradial ridges are developed. E_{1-2} and I_{1-2} are continuous in front of the glabella, and only one or perhaps two pits of E_2 are generally absent at the genal angle. The difference in size between the pits of the four outermost rows is not obvious, though those of E_1 and I_{1-2} become slightly larger posterolaterally. Radial arrangement of the fringe pits is not nearly so conspicuous as in later forms of *Broeggerolithus*, particularly outside E_1, and the radii may be straight or flexed slightly either backwards or forwards. Several auxiliary pits are present in E_2, and these are sometimes displaced slightly out of concentric line, either outwards or inwards. The number of pits present in each of the four outermost rows is as below ; no mode is given as this would be unjustified on the basis of the material available. $E_2 + e_2 = 27–28$, $E_1 + e_1 = 23–24$, $I_1 + i_1 = 23–24$, $I_2 + i_2 = 22–24$. The fringe notation for the lectotype is E_1 1–23, E_2 1–22 ; e_2 0, vi, x, xiii, xvi ; I_1 1–23, I_2 1–22 ; i_2 xx. I_3, and the area internal to it, is incompletely preserved but appears to extend from at least as far forwards as R12. There are nine pits along the posterior margin of the fringe.

On the underside of the fringe the girder, well developed centrally, becomes weaker near the genal angles where it is continuous with the longitudinal ridges on the genal spines, and two pseudo-girders, I_{1-2} and I_{2-3}, become stronger near the genal angles. All these concentric ridges carry longitudinal striae. In the median region of the lower lamella some of the pits of E_{1-2} and I_{1-2} are paired in shallow, radial sulci, and one pair of I_{1-2} pits has been found twinned ; the radial sulci quickly die out laterally.

In another specimen, which is only tentatively assigned to the species, BM. In. 52041 (Pl. 16, fig. 1), the pits of E_2 are noticeably smaller and more densely crowded, so that several are displaced out of line, though there is no suggestion of another concentric row. This specimen is so far unique, but may eventually prove to merit at least subspecific separation, though the general appearance is similar to that of *B. harnagensis* and, apart from E_2, all the concentric rows contain a comparable number of pits. The specimen is more noteworthy, however, for its retention of part of the test. The surface of the cheek-lobe shows vestigial coarse reticulation, but on microscopic examination the test proves also to be covered with minute, round punctae. A series of quite distinct punctae, larger and more irregular in both form and distribution, is situated between each of the hypostomal pits and the pitted area of the fringe, and may possibly denote the position of sensory hairs. An identical structure is noted later in the description of *Onnia superba*, and has not apparently been found previously in trinucleids.

The thorax is unknown.

The pygidium is triangular in outline, the maximum breadth being three times the length. The axis is about one-sixth of the total breadth, and triangular in plan, just attaining the tip of the pygidium. There are twelve or thirteen axial rings, the first two of which are completely and deeply delimited, the remainder becoming less distinct towards the tip. The pleural lobes are slightly swollen just outside the axial furrows and, again, near the margin, the position of which is marked by a small, raised rim. Apart from the articulating furrow only two pleural furrows are seen, continuous with their corresponding axial rings ; they become deeper laterally, but diminish in strength posteriorly. The border is, for the most part, steeply declined, except at and near the bluntly pointed tip of the pygidium, where its declination is much less.

HORIZON AND LOCALITIES. The species first appears in south Shropshire in the thin topmost layer of the Hoar Edge Grits; at this horizon, probably as a result of the shallow, sandy environment, it has not yet been found to be accompanied by *Reuscholithus* or any other trilobite, but the stratum is, nevertheless, taken as the basal bed of the Harnagian Stage at that point, following conformably upon the remainder of the Hoar Edge Grits, of Costonian age. For practical purposes the basal bed is included with the *Reuscholithus reuschi* Zone, as there is insufficient basis for erecting a *B. harnagensis* Zone. Immediately above the basal sandstone the species becomes more abundant in the grey shales and mudstones of the Harnage Shales proper, accompanied by *Reuscholithus reuschi*. It was from this horizon that the type-specimens were obtained, the type-locality being in the south bank of Coundmoor Brook, 1340 yards south-west of Harnage Farm. *B. harnagensis* has been found in numbers only in the Coundmoor Brook district of south Shropshire; farther south it is represented by a closely similar form described later as *B.* cf. *harnagensis*.

LECTOTYPE, here selected. BM. In. 42081 (Pl. 16, fig. 5), the cephalon figured by Bancroft (1929*a*, pl. 1, fig. 1).

PARATYPE. BM. In. 49024 (Pl. 16, fig. 13), the nearly complete pygidium figured by Bancroft (1929*a*, pl. 1, fig. 2).

FIGURED SPECIMENS. BM. In. 54029 (Pl. 16, fig. 9); doubtfully, BM. In. 52041 (Pl. 16, fig. 1).

DISCUSSION. The Shropshire species was recorded by Bancroft (1933: Table 3) from the Derfel Limestone of Bala, but material from that horizon has since been figured and described as *Salterolithus* cf. *harnagensis* by Whittington (*in* Whittington & Williams, 1955: 420, pl. 40, figs. 94–96, 100, 101) who has shown that several minor differences exist between the two forms. In particular we may note that the Bala specimens have fewer pits in I_1 and E_{1-2}, E_2 pits which are much smaller than those of adjacent rows, and that auxiliary pits of E_2 occur predominantly in the lateral parts of the fringe, whereas in the Shropshire species there may be several anteriorly. It seems likely that the two will prove eventually to be specifically distinct. The Derfel Limestone forms are believed to occur at or near the top of the Nant Hir Shales, belonging to the *Nemagraptus gracilis* Zone (Whittington & Williams, 1955: 397–398), and this horizon cannot be far removed from that of the earliest appearance of *B. harnagensis* in south Shropshire. There the basal Harnagian stratum forming the topmost Hoar Edge Grits is underlain by Costonian beds containing graptolites of the *N. gracilis* Zone and overlain by Harnage Shales belonging to the *Diplograptus multidens* Zone (Dean, 1958: 228), and it is not yet clear to which of the two graptolite zones it should be assigned.

Broeggerolithus cf. ***harnagensis*** (Bancroft)

(Pl. 16, figs. 7, 11)

1949. *Salterolithus* aff. *harnagensis* Bancroft: Bancroft, p. 291, pl. 10, fig. 15.

The southernmost occurrences of forms resembling *B. harnagensis* yet known are all in Neptunian dykes filling fissures in Uriconian rocks at the disused quarry on the southern flank of Hazler Hill, east of Church Stretton. All the specimens known belong to a form which Bancroft figured as *Salterolithus* aff. *harnagensis*, a name which implies that he considered it to be distinct from, though related to, *Broeggerolithus harnagensis* itself. He cited as differences (1949 : 291) the presence of an extra pit in E_1, and others in E_2 frontally, at or near the median line. However, other specimens from Hazler Hill show that the above features are not constant in all individuals, and in view of the variation shown by *B. harnagensis* it is considered unlikely that we are dealing with a different species. The lack of adequate well-preserved material makes certain specific identification inadvisable, but a smaller cephalon 10 mm. wide, BM. In. 50502, has the following estimated pit-count for the outermost rows $E_2 + e_2 = 24$, $E_1 + e_1 = 23$, $I_1 + i_1 = 21$, $I_2 + i_2 = 21$. These figures compare closely with those one might reasonably expect from an immature individual of *B. harnagensis*, and are very near to those given by Whittington (*in* Whittington & Williams, 1955 : 420–421) for the Derfel Limestone specimens, though the size of these is not stated.

FIGURED SPECIMENS. BM. In. 42093 (Pl. 16, fig. 11) ; BM. In. 50500 (Pl. 16, fig. 7).

Broeggerolithus? sp.

(Pl. 16, fig. 2)

From the type-locality of *Broeggerolithus harnagensis* in Coundmoor Brook there has been collected a unique cephalon which presents some difficulties with regard to generic classification. The cephalon, though slightly damaged, is apparently subsemicircular in outline, the median length much less than half the breadth, with the genal angles set far back so as to form exceptionally large " ears ". The glabella is incomplete but expands anteriorly and has a pair of deep apodemal pits just in front of a pair of similarly-sized occipital pits situated immediately inside the outer ends of the occipital furrow. The occipital ring is small and short, and there appears to have been an occipital spine, now broken off. The moderately convex cheek-lobes are smooth, separated from the glabella by very broad axial furrows which shallow anteriorly and contain deep, round hypostomal pits well forwards. The pleuroccipital furrow is narrow (*exsag.*) and deep ; both it and the small pleuroccipital segment extend to the fulcral sockets, situated only about one-third of the distance from the axial furrows to the lateral margin.

The fringe is fairly broad (*sag.*) anteriorly where there are four continuous rows of pits, E_{1-2} and I_{1-2}, and remains of even breadth as far as about R20 when it expands suddenly and markedly, extending about halfway from the lateral margin to the axial furrows and producing the large " ears " noted above. As far as can be seen the pits of the outer four, and perhaps five, rows are of almost similar size, those of E_2 being only very slightly smaller. Broad concentric " bands " are found on the smooth upper lamella between E_1 and I_1, and between I_1 and I_2. The number of pits in the outermost concentric rows is $E_2 + e_2 = 27$, $E_1 + e_1 = 25$, $I_1 + i_1 = 27$, $I_2 + i_2 = 24$. These figures show a generally higher count than the corresponding data for *B. harnagensis* but the number of pits along the posterior margin of the fringe, nine, is the same. The cephalon is generally similar in many respects to that of *B. harnagensis*, but a very conspicuous difference is the presence of several pits, equal in size to those of E_2, situated between E_1 and E_2. These do not displace the concentric line of E_2 outwards in any way, and the pit walls separating them from the pits of E_1 and E_2 are very thin, so that we can hardly consider that they are causing the production of an incipient E_3, the undoubted presence of which would necessitate the inclusion of the specimen in *Salterolithus*. The extra pits number four in the left half of the fringe, but there appear to be more in the right half, and, even though the main concentration is near the anterolateral angle of each half, the two halves are not symmetrical. In consequence it has been thought advisable merely to assign the specimen tentatively to *Broeggerolithus* until more material is available, though the random, asymmetrical arrangement of the fringe pits suggests that it may be an abberrant form possibly related to *B. harnagensis*.

HORIZON AND LOCALITY. Harnagian Stage, Zone of *Reuscholithus reuschi*, south bank of Coundmoor Brook, 1356 yards south-west of Harnage Farm.

FIGURED SPECIMEN. BM. In. 54030 (Pl. 16, fig. 2).

Broeggerolithus ulrichi (Bancroft)

(Pl. 17, figs. 10, 11)

1933. *Ulricholithus ulrichi* Bancroft, p. 2, table 2, MS. name only.
1949. *Salterolithus* (*Ulricholithus*) *ulrichi* Bancroft, p. 296, pl. 9, fig. 14.
1958. *Salterolithus* (*Ulricholithus*) *ulrichi* Bancroft : Whittard, p. 84, pl. 12, fig. 1.
1958. *Ulricholithus ulrichi* (Bancroft) : Dean, pp. 200–202, pl. 26, fig. 6.

DESCRIPTION. Owing to the fact that the holotype is merely an incomplete half of a cephalon preserved as an external mould, the following description is founded on additional topotype material.

Cephalic outline well rounded, almost semicircular but becoming straight sided posterolaterally ; its length, excluding occipital and genal spines, is rather more than half the maximum breadth. The glabella is moderately convex, slightly clavate anteriorly, and no median ocellus has yet been seen. No glabellar furrows have been found preserved, but most of the material available is crushed or incomplete. The cheek-lobes are smooth, gently convex, longer than broad, and separated from the glabella by broad, moderately deep axial furrows in which small, hypostomal pits are sited well forwards. The occipital ring is small, delimited by a shallow occipital furrow ; apparently there is an occipital spine, but it has not yet been found intact. The pleuroccipital furrow is shallow and the pleuroccipital segment small and narrow (*exsag.*). Beyond the pleuroccipital segment the posterior margins of the fringe are straight and sweep back gently towards the genal spines ; the latter are prismatic in cross-section, tapering from stout bases to slender points. Each has a median groove on its upper surface and curves outwards and backwards at about 20 degrees to the median line. The cephalic fringe is flat, broad, and of fairly even breadth ; it is moderately declined laterally and apparently less so anteriorly. Four rows of pits, E_{1-2} and I_{1-2}, are continuous in front of the glabella, which encroaches a little on the fringe causing some flexing forwards of the concentric rows of pits there. E_1 and I_1 consist of pits slightly larger than those of neighbouring rows ; the pits of I_2 are of similar size near the genal angle, but become smaller as they approach the median line. In general the pits of E_2 are somewhat smaller than those of E_1 and I_1, and they diminish slightly towards the genal angle. Interradial ridges are developed on a small scale but include only the rows E_{1-2} and I_1 ; in the case of E_1 they appear more conspicuous owing to the fact that the row is raised slightly above adjacent rows. The concentric lines of E_{1-2} and I_1 are set fairly close together, but I_2 is separated from I_1 by a relatively broad concentric band, corresponding in position with a poorly-developed pseudogirder on the underside of the fringe. The true girder, between E_1 and I_1, is strongly developed, but there is no corresponding feature on the upper lamella. The amount of well-preserved topotype material does not warrant the publication of figures showing the average number of pits present in the fringe, but a cephalon about 15 mm. wide has the following notation $E_1 = 1\text{–}22$; $E_2 = 1\text{–}19$; $e_2 = 0$, i, iii, iv ; $I_1 = 1\text{–}22$; $I_2 = 1\text{–}21$; $I_3 = 13\text{–}21$; $i_3 =$ xvii, xviii ; I_4 is represented only by a few pits in the angle formed by the cheek-lobe and the posterior margin of the fringe. The number of pits present does not appear to increase appreciably in larger individuals, and in one cephalon 24 mm. wide the number of pits in E_1 and I_1 is only 23 per row. Particularly characteristic is the presence of several auxiliary e_2 pits in front of the glabella ; some of these may be somewhat irregular in their arrangement, but they can hardly be considered as adventitious pits, and Bancroft's assertion that a few pits of E_3 may be present is thought to be unjustified. The usual number of pits along the posterior margin of the fringe is 6 or 7, and the average number of E_1 pits external posterolaterally near the genal angle appears to be 3. There is a small raised marginal rim to the fringe, and just below and outside this runs the marginal suture, which extends to the genal angle, where it turns inwards through rather more than a right-angle and almost immediately cuts the posterior margin of the fringe.

The thorax is unknown.

The pygidium is three times as broad as long, almost semi-elliptical in outline but with a bluntly-pointed tip. The front of the axis occupies about one-fifth of the maximum breadth, tapering and extending to the rear margin which is marked by a small raised rim. The axis is only slightly convex, and bounded by poorly-developed axial furrows. The pleural lobes are almost flat near the axis but become slightly swollen towards the margin. In addition to the articulating furrow there is one pair of pleural furrows ; these run straight outwards and slightly back from the axial furrows for about three-quarters of their length, and then, on encountering the swollen area of the pleural lobes, curve backwards to the margin. There are two pairs of faint rib furrows which become marked only at the margin which they meet close to, and just behind, the pleural furrows. The border of the pygidium is steeply declined, though slightly less so behind the termination of the axis.

HORIZON AND LOCALITIES. The type-locality is in the stream-section in Middle House Dingle, 120 yards west-north-west of Middle House, 3½ miles north of Welshpool, Montgomeryshire, where the species is found also in strata immediately underlying those of the type-locality. According to Bancroft the horizon is in the uppermost portion of the Harnagian Stage. *Broeggerolithus* [*Ulricholithus*] *ulrichi* was recorded by Bancroft (1949 : 296) from two localities in south Shropshire, both in the vicinity of Glenburrell Farm, Horderley. One locality is by the north-west side of the track 50 yards west-north-west of Glenburrell Farm, and the second is by the north-west side of the same track about 15 yards north-east of the first locality. The material from these beds is fragmentary and poorly preserved but appears to be at least close to *B. ulrichi*. The horizon of these specimens is the lowest part of the Glenburrell Beds, below the appearance of *Broeggerolithus broeggeri* at the base of the Soudleyan Stage, and their Harnagian age seems to be correct.

HOLOTYPE. BM. In. 42371.

FIGURED SPECIMENS. BM. In. 49708 (Pl. 17, fig. 10); BM. In. 54024 (Pl. 17, fig. 11).

DISCUSSION. It was stated by Bancroft (1949 : 295) that " *Ulricholithus* cannot be regarded as an early member of the genus *Broeggerolithus* which has reticulate ornamentation of the cephalon and in which stratigraphically early species are of notably smaller size than *Ulricholithus*. *Broeggerolithus* also has strongly elevated radial plates in E_1 and smaller modal numbers for the I_1 count ". After examination of topotype material the writer cannot agree with this argument, and Bancroft's inclusion of the species in *Salterolithus* must be rejected as there is no development of E_3. Apart from this, all the other characteristics, such as the development, even though on a small scale, of interradial ridges, the slight elevation of E_1 above adjacent rows, and the basic plan of four continuous rows of pits with a few pits of E_2 absent at the genal angles, indicate a close relationship to *Broeggerolithus* as typified by *B. broeggeri*, and *B. ulrichi* probably forms a link between that species and the earlier, more extreme development of *B. harnagensis*. None of the topotypes of *B. ulrichi* shows any trace of reticulation on the cephalon, but this is also true of most material belonging to the genus and cannot be considered of primary significance.

Broeggerolithus broeggeri (Bancroft)

(Pl. 16, figs. 3, 10)

1929*a*. *Cryptolithus broeggeri* Bancroft, p. 85, pl. 1, figs. 6–8.
1933. *Broeggeria broeggeri* (Bancroft) Bancroft, p. 2, tables 2, 3.
1935. *Broeggerolithus broeggeri* (Bancroft) Bancroft, p. 333.
1938*a*. *Cryptolithus broeggeri* Bancroft : Whittington, pp. 425, 428, 436, 450.
1940. *Broeggerolithus broeggeri* (Bancroft) : Whittington, p. 245.
1941. *Broeggerolithus broeggeri* (Bancroft) : Whittington, p. 24.
1949. *Broeggerolithus broeggeri* (Bancroft) : Bancroft, p. 298, pl. 9, figs. 4, 5.
1958. *Broeggerolithus broeggeri* (Bancroft) : Whittard, p. 89, pl. 12, figs. 7–13.
1958. *Broeggerolithus broeggeri* (Bancroft) : Dean, p. 203, pl. 26, fig. 7.

This abundant and well-known species was described in detail by Bancroft (1929*a*) and the lectotype has more recently been redescribed in modern fashion by Whittard (1958 : 89), so little need be added here. The lectotype is representative of the population at the type-locality, both in size and number of pits. The underside of the fringe of the species shows a strongly-developed girder between E_1 and I_1 extending as far as the genal angles, where it curves outwards in line with the splayed genal spines. Between I_1 and I_2 there is a pseudogirder which is moderately well developed posterolaterally but which dies out near the median line ; the position of the pseudogirder corresponds with a narrow, slightly-raised concentric ridge on the upper lamella. Whittard (1958 : 90), in describing material from the Shelve Inlier belonging to the species, has noted that three pits of E_1 may be external posteriorly, whereas Bancroft (1929*a* : 85) claimed " one or two (rarely more) "; in practice, specimens from south Shropshire with three pits external are not uncommon and may be regarded as part of the normal population.

HORIZON AND LOCALITIES. The type-locality is in the eastern bank of the small stream-section by the extreme north-east corner of Smeathen Wood, near Horderley, about 150 yards almost due south of Round House. One of the paratypes now lost (Bancroft, 1929*a* : pl. 1, fig. 8) originated from the exposure behind the western end of Glenburrell Farm, Horderley, a locality at which the species was said to be abundant (Bancroft, 1929*a* : 86). The horizon of all these type-specimens is in the upper half of the Glenburrell Beds, the lower half of the Soudleyan Stage, to which the term *Broeggerolithus broeggeri* Zone is applied. The species can also be found at several other localities near Glenburrell Farm and in the bed of the River Onny nearby, all of them at the same horizon. It occurs also in the Glenburrell Beds exposed in the stream a quarter of a mile due west of Long Lane Quarry, north-west of Craven Arms.

LECTOTYPE, selected by Whittard (1958 : 88). BM. In. 42077 (Pl. 16, fig. 3), the cephalon figured by Bancroft (1929*a*, pl. 1, fig. 6).

PARATYPES. The other two specimens figured by Bancroft (1929*a*, pl. 1, figs. 7, 8), comprising a pygidium and incomplete cephalon, have not yet been traced, and are probably lost.

FIGURED SPECIMEN. BM. In. 50831 (Pl. 16, fig. 10).

***Broeggerolithus* cf. *broeggeri* (Bancroft)**

(Pl. 16, figs. 4, 8, 14)

In his original description of *Broeggerolithus broeggeri*, Bancroft (1929*a* : 86) emphasized that the specific name was not to be applied to specimens unless all or nearly all of them, even though resembling *B. broeggeri* in most respects, exhibited what he called " intercalated pits in front of the glabella ", now termed auxiliary pits. We are thus left with numerous individuals, some of them occurring in company with *B. broeggeri*, which show only relatively small, though constant, differences from that species. A whole individual typical of this group is figured here (Pl. 16, figs. 4, 8) from the type-locality of *B. broeggeri* itself. The cephalon is relatively longer than in *B. broeggeri* forma typica, the length of 9 mm. (excluding occipital spine) being half the breadth. This is noticeably more than is usual, but as there is some variation within the species this cannot be considered a reliable specific distinction. The notation for the fringe of the figured specimen is $E_1 = 1–22$; $E_2 = 1–19$; $I_1 = 1–22$; $I_2 = 1–20$; $I_3 = 11–21$; $I_{4–5}$ are represented by a few pits in the angle formed by the cheek-lobe and the posterior margin of the fringe.

This is remarkably close to the notation given by Whittard (1958 : 90) for the lectotype of *B. broeggeri*, and the absence of any auxiliary pits from in front of the glabella is the only feature to distinguish the form from *B. broeggeri* ; this is not considered sufficient to merit specific separation.

Trilobites generally similar to the above, though poorly-preserved, have been found in the *Glyptocrinus* Flags of the Chatwall district in the northern part of the Caradoc Area, and the cephalon of one is figured here (Pl. 16, fig. 14). It has been suggested (Dean, 1958 : 204) that they may possibly indicate the presence of the *B. broeggeri* Zone there. If this is so, then part at least of the *Glyptocrinus* Flags must be diachronic, as the same lithological horizon belongs to the *Broeggerolithus soudleyensis* Zone, Upper Soudleyan, farther south in the Onny Valley.

HORIZON AND LOCALITIES. In. 48937 is from the stream-section at the extreme north-eastern corner of Smeathen Wood, near Horderley, 150 yards south of Round House ; the horizon is the *B. broeggeri* Zone of the Soudleyan. In. 51447 is from the *Glyptocrinus* Flags, ? *B. broeggeri* Zone, by the south side of the road 170 feet north-north-east of Chatwall Farm, Chatwall.

FIGURED SPECIMENS. BM. In. 48937 (Pl. 16, figs. 4, 8) ; BM. In. 51447 (Pl. 16, fig. 14).

Broeggerolithus constrictus Bancroft

(Pl. 16, figs. 6, 12)

1933. *Broeggeria constricta* Bancroft, table 3. MS. name only.
1949. *Broeggerolithus constrictus* Bancroft, p. 298, pl. 9, fig. 38.

Bancroft's account of the species was brief and included only the following diagnosis : " this group is characterized by having three pits of E_1 external towards the genal angle, by an abrupt constriction of the fringe behind the most posterior pit-radius with both E_1 and E_2, and by the unusual triangular contour of the pygidium " (1949 : 298). His description of the place of origin of *B. constrictus* referred to " the more important type-locality " near Ceunant, in the Welshpool District, but as he figured and described only one specimen, which thus became the holotype, one can only conclude that he had intended to base his species on a number of syntypes from differing localities. The holotype is an incomplete cephalon which does not show the fringe pits in front of the glabella. The rearmost portion of the fringe margin is obscure, and it is not quite clear whether the so-called constriction behind the rearmost pit of E_1 is actually present, or whether it is due to the breaking away of a small fragment of the test. Topotype specimens suggest that the latter may be the case, and show also that the constriction behind the rearmost pit of E_2 is not always so marked as in the holotype. In front of the glabella of the holotype it is estimated that three radial rows of pits are incomplete or absent, the remaining radial rows commencing in front of the axial furrows ; thence towards the genal angle the number of primary radial rows (R) present in I_2, I_1, E_1 and E_2 respectively is 16, 16, 15 and 13, with only an occasional auxiliary pit in I_2 and E_1. I_3 is developed only from about R13 to the posterior margin. The marginal rim of the fringe is usually slightly raised, more so in topotype material than in the holotype, so that E_2 appears to be depressed, and there is a raised concentric ridge on the upper lamella between I_1 and I_2. Interradial ridges are strongly developed along most of E_1, especially anterolaterally. The surface of the cheek-lobes of the holotype shows slight traces of reticulation which is more evident on some of the topotype specimens. Near the intersection of the axial and pleuroccipital furrows the reticulation is fairly coarse, becoming finer towards the fringe both anteriorly and laterally; similarly there is a gradation from coarse to fine reticulation from the rear of the glabella towards the front.

The thorax is unknown.

Although Bancroft's diagnosis of *B. constrictus* referred to the " unusual triangular contour of the pygidium ", no pygidium was figured by him. No topotype pygidium has been found in his collection, so that a detailed description cannot be written.

HORIZON AND LOCALITIES. The type-locality is in the stream-section 515 yards west-south-west of Ceunant, four miles north-north-east of Welshpool, Montgomeryshire. The horizon was referred to by Bancroft (1949 : 299) as the *Broeggerolithus constrictus* Beds, at the base of the Soudleyan Stage, strata to which the name *Broeggeria broeggeri-constricta* Beds had been applied earlier (Bancroft, 1933 : Table 3). A locality in the Onny Valley was also claimed by Bancroft (1949 : 298) as having yielded *B. constrictus*, and from his information this can now be localized as being in the bed of the River Onny near the north bank, just east of the river-fence junction 55 yards almost due south of Round House, Horderley. The material from this locality has been examined by the writer and is considered to be probably referable to *Broeggerolithus broeggeri*, though the specimens are poorly preserved. The south Shropshire occurrence is in strata belonging to the Soudleyan Stage, Zone of *Broeggerolithus broeggeri*, and although these undoubtedly form part of the Lower Soudleyan it is not considered that the name *B. constrictus* Beds has any value. No records of the species are yet known outside the Onny Valley and the Welshpool District.

HOLOTYPE. BM. In. 42101 (Pl. 16, fig. 6).

FIGURED SPECIMEN. BM. In. 51883 (Pl. 16, fig. 12).

DISCUSSION. *Broeggerolithus constrictus* is of the same geological age as *B. broeggeri*, a species which it much resembles, and of which it may possibly prove to be merely a variety, though for the present the two are retained as separate species. The following features have been found useful in distinguishing them.

Usually *B. constrictus* has a slightly longer cephalon than *B. broeggeri*, though it may vary slightly; in this respect, some forms referred earlier to *B.* cf. *broeggeri* have a longer cephalon than the species itself. The glabella and cheek-lobes of topotype specimens of *B. constrictus* usually have a reticulate surface, even in mature individuals, contrasting with the smooth surface of these parts of the exoskeleton in *B. broeggeri*. Reticulation has not been found on the specimens referred by Bancroft to *B. constrictus* from the Onny Valley. The most noticeable difference between the two species is the smaller pit-count of *B. constrictus*, which has several fewer pits in the three outermost rows.

Broeggerolithus soudleyensis (Bancroft)

(Pl. 17, figs. 1–9, 17)

1929*a*. *Cryptolithus soudleyensis* Bancroft, p. 86. pl. 1, figs. 9–11.
1933. *Broeggeria soudleyensis* (Bancroft) Bancroft, table 2.
1935. *Broeggerolithus soudleyensis* (Bancroft) Bancroft, p. 334.
1938*a*. *Cryptolithus soudleyensis* Bancroft : Whittington, p. 451.
1940. *Broeggerolithus soudleyensis* (Bancroft) : Whittington, p. 245.
1941. *Broeggerolithus soudleyensis* (Bancroft) : Whittington, p. 27.
1945. *Broeggerolithus soudleyensis* (Bancroft) : Bancroft, pp. 210, 211, 239.
1958. *Broeggerolithus soudleyensis* (Bancroft) : Whittard, p. 91, pl. 12, fig. 14.
1958. *Broeggerolithus soudleyensis* (Bancroft) : Dean, p. 204, pl. 26, fig. 8.
1958. *Broeggerolithus* aff. *soudleyensis* (Bancroft) : Dean, pp. 207, 222.

DESCRIPTION. In the absence of suitable syntypes the following description is founded on topotype material.

Cephalon almost semielliptical in plan, slightly angular, the length being less than half the maximum breadth. The glabella is clavate anteriorly; bears a small median ocellus, and is strongly convex, standing high above the cheek-lobes from which it is separated by broad, moderately deep, gently curving axial furrows with deep, round, hypostomal pits situated well forwards A fairly deep occipital furrow marks off the small occipital ring which is produced backwards and upwards into an occipital spine ; the total length of the occipital ring and spine is about half that of the glabella. The fringe is narrow (*sag.*) in front of the glabella, widening slightly towards the genal angles. The pleuroccipital furrow is moderately deep, becoming shallower laterally ; it delimits a narrow pleuroccipital segment which is transversely straight as far as the fulcral sockets, beyond which the posterior margins of the fringe run backwards only slightly to the genal spines, the so-called " ears " being of very small size. Genal spines are rarely found intact ; they are divergent rearwards, and the longest yet seen is about the same length as the cephalon.

In front of the glabella, where several pits of E_2 are absent, the pits of all the concentric rows present are of similar size, but anterolaterally those of E_1 and I_1, particularly the latter, become larger. Over most of the fringe there is a conspicuous radial arrangement of pits and interradial ridges are developed, particularly in E_1 which is raised above the level of the adjacent concentric rows. There is a raised concentric ridge between I_1 and I_2 which corresponds in position with a pseudogirder, developed laterally, on the lower lamella of the fringe. The true girder, between E_1 and I_1, extends as far as the base of the genal spines, but is only strongly developed as far as the anterolateral angles. The notation for the fringe of a typical topotype cephalon (Pl. 17, figs. 9, 17) is $E_1 = 0\text{–}20$; $E_2 = 4\text{–}19$; $I_1 = 0\text{–}21$; $I_2 = 0\text{–}20$; $I_3 = 16\text{–}20$; $i_3 = \text{xvi}$; there is then a triangular area between the cheek-lobe and the posterior margin of the fringe which contains 9 pits. Particularly noticeable is the absence of auxiliary pits from nearly all parts of the fringe. There are seven pits along the posterior margin of the fringe.

The thorax and pygidium have not been found sufficiently well preserved for description.

A well-preserved cephalon about 11 mm. wide is figured here from the Upper Longvillian Substage (Pl. 17, figs. 2–4). The cephalic outline is slightly less angular anteriorly than the topotype just described and the pit-count is somewhat smaller, but as the cephalon is of a smaller individual this is not considered to be of specific importance. Three pits of E_2 are absent at the genal angle in the Upper Longvillian specimen but this number may vary from one to three in the species. The pit-notation is E_1 1–18, E_2 4–15, e_1 xv, e_2 xv; I_1 1–18; I_2 1–18; I_3 11–18, i_3 xi, xiii, xiv, xviii; internal to I_3 the triangular area between the fringe margin and the cheek-lobe is occupied by eight pits, and there are six pits situated along the posterior margin of the fringe.

Distribution. The species appears first as uncommon individuals accompanying *Broeggerolithus broeggeri* in the Lower Soudleyan of the Onny Valley. In the Upper Soudleyan *B. soudleyensis* becomes the dominant trilobite, sufficiently so as to be used as zonal index. It is widespread in the Caradoc area of Shropshire where it is found at many points, for example the Onny Valley south-east of Glenburrell Farm, Horderley, and the quarries a quarter-mile north-west of Sibdon Castle, near Craven Arms, and is also recorded from the Shelve Inlier and various parts of North Wales. Rare specimens have been found in the *Alternata* Limestone (Upper Longvillian) of Soudley Quarry, where they are accompanied by *Broeggerolithus longiceps* (Bancroft) and *Kjaerina bipartita* (Salter); this record is unusual for south Shropshire, but *B. soudleyensis* has been recorded from both the Lower and Upper Longvillian Substages of the Llansantffraid-ym-mechain district, Montgomeryshire (Whittington, 1938*a* : 451).

Type specimens. Of the three syntypes figured by Bancroft in his original description, only two have been recovered; both are poorly preserved and neither is figured here. They are now numbered BM. In. 49025 (probably Bancroft, 1929*a*, pl. 1, fig. 10) and BM. In. 42078 (Bancroft, 1929*a*, pl. 1, fig. 11). Both specimens are from the Soudley Sandstone, Upper Soudleyan Stage, of Soudley Quarry, just south-east of Soudley Pool, between Hope Bowdler and Ticklerton, about twenty feet below the base of the *Alternata* Limestone at that point. Neither specimen is considered to show any sufficiently diagnostic features of the species, so it is not proposed to select either as lectotype. The portion of an incomplete cephalon figured later by Bancroft (1949, pl. 9, fig. 6) from the Upper Soudleyan at the small quarry 100 yards south-east of Glenburrell Farm, Horderley, is also lost.

Figured specimens. BM. In. 49314 (Pl. 17, fig. 1); BM. In. 50584 (Pl. 17, figs. 2–4); BM. In. 51446 (Pl. 17, fig. 5); BM. In. 51445 (Pl. 17, fig. 6); BM. In. 50586 (Pl. 17, fig. 7); BM. In. 52856 (Pl. 17, fig. 8); BM. In. 54025 (Pl. 17, figs. 9, 17).

Discussion. *Broeggerolithus soudleyensis* bears a considerable resemblance to *B. broeggeri*, to which it is obviously related, but it is easily distinguished by the number of pits of E_2 absent from in front of the glabella. In his original description Bancroft (1929*a* : 86, 87) gave the number of pits absent as from four to eight, and in general it may be stated that the earliest known forms from the *Broeggerolithus broeggeri* Zone have a smaller number of pits absent anteriorly than later ones, but there is no uniform tendency to increase the number of pits lost, as the maximum number known to be absent in Upper Soudleyan specimens is eight, whilst in the Upper Longvillian it is six. From a later paper by Bancroft (1935 : 334) it appears probable that he did not regard the earliest forms from the *B. broeggeri* Zone as belonging to *B. soudleyensis*, but believed them to be what he called " rare mutations " of *B. broeggeri*. In the present paper the species is interpreted more widely so as to include all those forms in which from one to eight pits of E_2 are absent frontally. A more extreme example of the variation to be expected is shown by a fringe (Pl. 17, fig. 8) in which another break, from R5 to R6, occurs in E_2, in addition to that immediately in front of the glabella.

Broeggerolithus globiceps (Bancroft)

(Pl. 17, figs. 13, 15, 16)

1929*a*. *Cryptolithus globiceps* Bancroft, p. 88, pl. 2, figs. 1, 2.
1938. *Cryptolithus globiceps* Bancroft : Whittington, p. 53, pl. 6, fig. 1.
1938*a*. *Cryptolithus globiceps* Bancroft : Whittington, p. 450.
1940. *Broeggerolithus globiceps* (Bancroft) Whittington, p. 245.
1947. *Broeggerolithus globiceps* (Bancroft) : Harper, pp. 155, 172.
1958. *Broeggerolithus globiceps* (Bancroft) : Dean, p. 206, pl. 26, fig. 9.

DESCRIPTION. Cephalic outline is slightly subangular anterolaterally, but is generally fairly well rounded except for a small portion of the fringe in front of the glabella where the margin is transversely straight owing to the absence there of a few, normally 3, pits of E_2. The total length, excluding the occipital ring, is more than half the maximum breadth. The glabella is usually large, strongly convex, and stands high above the moderately swollen cheek-lobes. The anterior portion of the glabella encroaches on to the fringe, being accommodated by the flexing forwards of the concentric rows of pits ; the posterior portion, excluding the occipital ring, extends well to the rear of the pleuroccipital segment. Glabellar furrows are represented only by a pair of basal apodemal pits, just behind which is situated a pair of smaller, slit-like occipital pits. The shallow occipital furrow and small occipital ring are directed backwards and upwards at about 45 degrees to the horizontal, and there is a small occipital spine in the same plane. The axial furrows are gently convex outwards, broad and only moderately deep, with small, round, deep hypostomal pits at their outer ends. The broad, shallow pleuroccipital furrows and narrow (*exsag.*) pleuroccipital segments extend about half-way from the axial furrows towards the lateral margin. Beyond the fulcral sockets the posterior margins of the fringe are straight, directed backwards slightly towards the bases of the genal spines and forming very small " ears ". The genal spines themselves are prismatic, flat on top, slightly curved, and strongly splayed rearwards. The marginal suture is of the normal trinucleid type.

The fringe is generally flat, declined gently in front of the glabella and much more strongly at and near the genal angles. In front of and adjacent to the glabella the concentric rows E_{1-2} and I_{1-2} contain pits of equal size, but laterally those of E_1 soon become larger and maintain a uniformly large size from about R7 or R8 to the genal angle. The pits of I_1 begin to become noticeably larger and polygonal from about R15 onwards, and by the time they reach the genal angle may be slightly larger even than those of E_1. Interradial ridges are developed in the three outermost rows, being more conspicuous in E_1 which is slightly raised above the remainder of the upper lamella. The concentric ridge between I_1 and I_2 is not conspicuous. Insufficient well-preserved material has been found to justify the publication of average pit counts for the various rows, but the notation for the lectotype is E_1 0–21, E_2 2–20 ; e_1 xx, xxii ; I_1 0–22, I_2 0–21, I_3 13–22 ; i_1 xix, i_2 xxi, i_3 xxi. I_4 consists of about 7 pits from R18, and I_5 is represented by 2 or 3 small pits. The number of pits of E_2 absent from in front of the glabella is usually three, and the point where E_2 commences is marked by a small break in the line of the cephalic margin. At and near the genal angles four or five pits of E_2 and e_2 are more commonly absent, but this number may be as small as three. The number of pits along the posterior margin of the fringe is usually seven or eight. A well-preserved underside of the fringe has not yet been found, but external moulds show that between E_1 and I_1 there is a strong girder which is particularly well developed anteriorly. A moderately strong pseudogirder occurs between I_1 and I_2, whilst there is a suggestion of another pseudogirder posterolaterally between I_2 and I_3.

The thorax is not yet known, and no sufficiently well-preserved pygidium is available for description.

HORIZONS AND LOCALITIES. The type-locality is situated just east of the south-western corner of Rookery Wood, three-quarters of a mile south-east of Horderley ; the horizon is in the Lower Longvillian Substage, associated with *Dalmanella lepta* (Bancroft). Recently it has been found more convenient to group together as one horizon within the Lower Longvillian Bancroft's two discrete Zones of *Wattsella indica* and *W. lepta*, both in south Shropshire and at Welshpool (Dean, 1958 : 206 ; Cave & Dean, 1959 : 297). *Broeggerolithus globiceps* is taken as index-fossil for the Lower Longvillian of south Shropshire (Dean, 1958 : 206) and other localities where it is to be found include the large quarry by the roadside 280 yards south-east of Glenburrell Farm, Horderley ; the quarry by the west side of New House, 625 yards south-east of Glenburrell Farm ; the disused railway cutting by the south-west bank of the River Onny between points opposite Glenburrell Farm and New House ; Long Lane Quarry, two-thirds of a mile south-west of Cheney Longville ; the old quarries in the eastern part of Longville Plantation, respectively 720 yards north-west and 740 yards west-north-west of the Earthwork at Cheney Longville ; and the quarry by the east side of the road 590 yards east-north-east of Cwm Head Farm, one and a half miles north-east of Horderley.

The species has not yet been found in any of the other outcrops of the Caradoc Series in England, but it has been recorded from various parts of North Wales including the Llanfyllin District of the Berwyn Hills, and the Pwllheli District.

LECTOTYPE, here selected. BM. In. 42076 (Pl. 17, fig. 15), an incomplete cephalon, preserved as an internal mould, figured by Bancroft (1929*a*, pl. 2, fig. 1) and, more recently, by Dean (1958, pl. 26, fig. 9).

PARATYPE. BM. In. 42075, an incomplete cephalon figured by Bancroft (1929*a*, pl. 2, fig. 2). The glabella of this specimen is slightly distorted and foreshortened, so that the projection of the posterior portion of the glabella behind the pleur-occipital segment is not apparent.

FIGURED SPECIMENS. BM. In. 49315 (Pl. 17, fig. 13); BM. In. 49321 (Pl. 17, fig. 16).

DISCUSSION. *Broeggerolithus globiceps* possesses certain features, such as well-developed interradial ridges, a raised E_1 row, and a general lack of auxiliary pits, which link it with *Broeggerolithus broeggeri*, but it is easily distinguished by the longer, more rounded cephalon, the conspicuous, tumid glabella, and by the absence of some pits of E_2 in front of the glabella. This last feature is reminiscent of *Broeggerolithus soudleyensis*, but the latter species has a much smaller number of fringe-pits as well as a shorter, more angular cephalon and a smaller glabella.

Broeggerolithus sp. (? nov.)

(Pl. 17, fig. 12)

Associated with *Broeggerolithus globiceps* (Bancroft) at its type-locality is another trinucleid, referred to *Broeggerolithus* (*s.s.*) which is represented only by a well-preserved half-fringe and incomplete glabella. In front of the glabella four concentric rows of pits are continuous, and contain pits of equal size. Laterally and postero-laterally the pits tend to increase in size, particularly those of E_1 and I_1 which are larger than those of the other rows, and which are of about equal size at the genal angle. E_1 is slightly elevated and interradial ridges are developed between the radial rows of the three outermost rows; the apex of each interradial ridge is situated between E_1 and E_2. The radial arrangement of pits is pronounced, but those of R6 are unevenly distributed; this is believed to be due to a slight malformation or injury, and corresponds with a small unevenness in the otherwise smooth margin of the fringe. The fringe-notation is $E_1 = 1–19$, $E_2 = 1–18$; $I_1 = 1–20$, $I_2 = 2–19$, $I_3 = 10–16, 18, 19$; $i_3 = xv, xvi$. I_4 is represented by 5 pits, irregularly arranged, from R16 outwards, and the remaining pits comprise a triangular cluster of five in the angle between the posterior margin of the fringe and the cheek-lobe. Only one pit of E_1 is external at the genal angle, and there are eight pits along the posterior margin of the fringe, which is straight and directed only slightly backwards to the genal angle.

HORIZON AND LOCALITY. The exposure in Rookery Wood, three-quarters of a mile south-east of Horderley, just east of the south-western corner. The horizon is in the middle subdivision of the Lower Longvillian Substage, characterized by *Dalmanella lepta* and *D. indica*.

FIGURED SPECIMEN. BM. In. 49313.

DISCUSSION. This form of *Broeggerolithus*, which may be new, differs from the associated *B. globiceps* in having a complete development of E_2 in front of the glabella, fewer pits of E_1 external at the genal angle, and a generally smaller pit count. The inadequate material makes comparison of the glabella in the two forms impossible, and it is not clear what relationship exists between them. Bancroft (1929*a*: 89) stated that *B. globiceps* occurred with a more abundant form, the fringe of which had a continuous E_2 row and was otherwise indistinguishable from that of *B. globiceps*. He regarded the two as members of the same dimorphic species, but if the form referred to by him is in fact the same as that figured here, it is considered that the differences are probably sufficient to justify specific separation when more material is available.

Broeggerolithus simplex sp. nov.

(Pl. 17, fig. 14)

Derivation of name. *simplex* (Lat.) = simple, from the relatively uncomplicated arrangement of the fringe-pits.

Description. Outline of cephalon is bluntly pointed in front, and subangular anterolaterally. The median length, excluding occipital spine, is half the maximum breadth of 12 mm. The glabella is not preserved in the only specimen available, but the left cheek-lobe is intact, showing it to be only moderately convex. The fringe is flat and of even breadth as far as the anterolateral angles where it expands towards the posterior margin. In the frontal part of the fringe, as far as the anterolateral angles, the pits of the four continuous, concentric rows are of equal size, but towards the genal angles at least those of I_{1-2} become conspicuously larger. A slightly raised concentric ridge is developed posterolaterally on the upper lamella between I_1 and I_2. Small interradial ridges are situated between the radial rows of pits in E_{1-2} and I_1, which thus appear to lie in shallow radial suci, but concentric row E_1 is not raised above its neighbours and the height of only a few interradial ridges increases very slightly at the line of E_1. The posterior margins of the fringe are directed outwards and backwards sharply to the genal angles, forming moderately large " ears "; the genal spines are not preserved in the holotype.

The state of preservation of parts of the fringe makes it difficult to decipher the entire notation, but as far as can be determined it is as below. The large number of radial rows of pits is particularly conspicuous, though not very different from *B. broeggeri*. $E_1 = 1–22$, $E_2 = 1–21$; $I_1 = 1–22$, $I_2 = 1–19, 21, 22$, $I_3 = 12–20$; $i_3 = \text{xvii}$. Extension of the notation to the rows internal to I_3 has not proved practicable. Only one pit of E_1 is external at the genal angle, and the number of pits arranged along the posterior margin of the fringe is about eight.

The undersurface of the fringe, the thorax and the pygidium are not yet known.

Horizon and locality. The type-locality is the same as that for *Broeggerolithus globiceps* (Bancroft), namely, just east of the south-western corner of Rookery Wood, three-quarters of a mile south-east of Horderley. The horizon is the Zone of *Dalmanella indica* and *D. lepta*, in the Lower Longvillian Substage. Fragmentary evidence of what may prove eventually to be the same species has been found in the *Dalmanella horderleyensis* Zone of the Lower Longvillian Substage in the Onny Valley between Glenburrell Farm and New House, and at Long Lane Quarry, two-thirds of a mile south-west of Cheney Longville.

Holotype. BM. In. 50614. This is the only specimen as yet definitely assigned to the species.

DISCUSSION. *Broeggerolithus simplex* is a distinctive small form and is unlikely to be confused with any of the contemporaneous Lower Longvillian trinucleids. It is only with hesitation that the species is included in Group 2 of *Broeggerolithus*, as it possesses certain features which are more reminiscent of species in Group 3. These are: a fairly flat fringe in which E_1 is not raised above other rows, and the posterior prolongation of the genal angles to form moderately large " ears ". Some of the interradial ridges are, however, slightly higher at the line of E_1, as in *Broeggerolithus* (*s.s.*), and the species is probably best regarded as intermediate between the two groups, or an early member of Group 3.

Whittington (1938 : 52, 53) has referred to trilobites which he called *Cryptolithus* cf. *gibbifrons* (McCoy) from the Lluest Quarry, Llanfyllin, Montgomeryshire, where they are accompanied by *Broeggerolithus globiceps* and other Lower Longvillian fossils including *Dalmanella horderleyensis* (Whittington). These forms were said to have four concentric rows of pits with conspicuous concentric arrangement in front of the glabella, and only one or two pits of E_1 external at the genal angle. The name used by Whittington was based on Bancroft's usage of *C. gibbifrons*, a term discussed earlier in this paper (page 104), and it seems more likely that the species in question might be either *Broeggerolithus* sp. (? nov.) or *B. simplex* sp. nov.

Broeggerolithus longiceps (Bancroft)

(Pl. 18, figs. 1, 4–6, 10)

1929*a*. *Cryptolithus longiceps* Bancroft, p. 89, pl. 2, figs. 3, 4.
1940. *Broeggerolithus longiceps* (Bancroft) Whittington, p. 245.
1945. *Broeggerolithus longiceps* (Bancroft) : Bancroft, p. 249.
1958. *Broeggerolithus longiceps* (Bancroft) : Dean, p. 207, pl. 26, fig. 10.

DESCRIPTION. Owing to the incompleteness of the type-material the following is based on both lectotype and topotype specimens.

The cephalon is usually almost semicircular in plan, though occasionally it may be slightly subangular anterolaterally and in front of the glabella; the median length, excluding the occipital spine, is half the maximum breadth. The glabella is long and high, swollen anteriorly, where it encroaches on, and slightly overhangs, the fringe, and becomes narrow at the occipital furrow. This last is shallow and both it and the small occipital ring, which is produced into a small occipital spine, are in a plane directed backwards and steeply upwards. The internal mould shows a pair of small, basal apodemal pits situated just in front of the occipital furrow, in the rear half of which is a pair of slit-like occipital pits. There is a small ocellus at the apex of the glabella about its mid-point. The axial furrows are broad, gently convex outwards and only moderately deep, a feature usually exaggerated by crushing. The cheek-lobes are plump and, together with the glabella, often carry coarse reticulation, particularly when preserved in limestone. The pleuroccipital furrow is broad (*exsag.*) and shallow, bordering a narrow (*exsag.*) pleuroccipital segment; the two run outwards, curving forwards very slightly, as far as the fulcral sockets, from which points the posterior margins of the fringe run outwards and sharply backwards to the bases of the backwardly-splayed genal spines, forming "ears" of fairly large size.

The fringe is flat and moderately broad (*exsag.*), becoming narrower anteriorly and broader towards the genal angles. From the limited uncrushed material available it is apparently only gently declined, both anteriorly and laterally. The four outer rows of pits are continuous in front of the glabella, where they consist of pits of equal size. Posterolaterally the pits of E_1 and I_{1-2} become larger, particularly those of I_1 which are conspicuously large near the genal angle. The upper lamella is generally smooth, interradial ridges being developed only on a small scale, so that from I_1 outwards the radial rows appear to be set in shallow sulci. No concentric row is raised above the others as happens in earlier species of *Broeggerolithus*, nor is I_1 depressed as claimed by Bancroft, though this may have appeared to be the case owing to the fact that a concentric ridge is noticeably developed between I_1 and I_2. A marginal rim of similar height is present, and there is another concentric ridge, less well developed, between E_1 and I_1; on the underside of the fringe the latter corresponds in position with a girder which is particularly well marked anteriorly and continued as a ridge on the underside of the genal spine. A smaller pseudogirder is present posterolaterally between I_1 and I_2. The usage of the normal fringe-notation presents some difficulties in the posterolateral parts of the fringe where, at first sight, there appear to be some auxiliary pits in E_2. There the pits form two sets of radiating lines in the outer part of the fringe, intersecting at an angle of about 60 to 70 degrees, and it may be difficult to decide which of the two should be interpreted as being continuous with the anterior radii. For the purpose of the following notation the radial rows in E_{1-2} and I_1 regarded as true radii are those which become progressively less divergent as they approach the genal angle. The pattern of fringe-pits in early Ordovician trinucleids is usually relatively simple, but in the earlier species of *Broeggerolithus* the problem outlined above is found on a small though increasing scale. In *B. longiceps* one is forced to regard as true radii those radial rows which are straight as far as the I_{1-2} pseudogirder, but which then flex forwards sharply. Using this method of interpretation the radii are seen to extend nearly to the genal angle, the apparent almost quincuncial arrangement being only superficial and auxiliary pits uncommon. The fringe notation for specimen BM. In. 52058, a typical mature topotype cephalon 24 mm. wide, is E_1 0–22, E_2 0–19; e_2 xviii, xix; I_1 0–23, I_2 0–22; i_2 ix, x. I_3 is represented by about 11 pits from R12 outwards, and there are about seven small pits in the I_4 region.

The number of adequately-preserved cephala is not large, but as far as can be judged the average number of pits in the principal rows of an adult specimen is $E_1 + e_1 = 24$, $E_2 + e_2 = 22$, $I_1 + i_1 = 23$, $I_2 + i_2 = 22$, $I_3 + i_3 = 12$ or 13. What is probably a small holaspid cephalon, 13 mm. wide, has the following pit-count in the four outer rows: $E_1 + e_1 = 21$, $E_2 + e_2 = 20$, $I_1 + i_1 = 21$, $I_2 + i_2 = 22$.

The thorax is unknown.

No pygidium was described by Bancroft, and none which can be definitely ascribed to the species is yet available. A few indifferently preserved pygidia of typical *Broeggerolithus* aspect have been found in the *Alternata* Limestone of the

Soudley district, but as more than one species of the genus is present there, it would be dangerous to assume they belong to *B. longiceps*.

HORIZONS AND LOCALITIES. The lectotype was collected from the exposure in the small stream by the west side of the road from Horderley to Marchbrook, about 480 yards north-north-east of Whittingslow. The locality is in the *Alternata* Limestone, the lower part of the Upper Longvillian Substage, and the species is found at this horizon at various localities throughout the Caradoc District, for example, the upper part of the old quarry by the east side of Soudley Pool, between Hope Bowdler and Ticklerton ; in the cutting 200 feet south-east of Chatwall Hall ; in the south side of the disused railway-cutting by the south bank of the River Onny, 175 yards south-south-east of New House, Horderley ; and in the sides of Longville Lane, 445 yards north-west of the " Earthwork " at Cheney Longville. *Broeggerolithus longiceps* is also found, though less commonly, in the upper part of the Upper Longvillian Substage, comprising strata with *Kjaerina typa* Bancroft and *K. geniculata* Bancroft. At this horizon it is found, for example, in the north-east bank of the stream 280 yards south-east of New House, west of Marshbrook.

LECTOTYPE, here selected. BM. In. 42073 (Pl. 18, fig. 6), an almost complete cephalon preserved as an internal mould and figured by Bancroft (1929*a*, pl. 2, fig. 3).

PARATYPE. The other specimen figured by Bancroft (1929*a*, pl. 2, fig. 4), and comprising the external mould of a glabella and occipital ring, has not yet been traced.

FIGURED SPECIMENS. BM. In. 50591 (Pl. 18, fig. 5) ; BM. In. 50661 (Pl. 18, figs. 1, 10) ; BM. In. 50739 (Pl. 18, fig. 4).

DISCUSSION. *Broeggerolithus longiceps* differs considerably in detail from most Lower Longvillian species of the genus, but has some features in common with *B. simplex* sp. nov. However, the Upper Longvillian form is easily distinguished by its more rounded cephalon with large " ears ", together with fewer pits in E_2 and more in I_1. *B. longiceps* is also an apparently larger form than any of those in the Lower Longvillian, but it is not clear whether this is due to its occurrence in a more amenable environment or not.

Broeggerolithus transiens (Bancroft)

(Pl. 18, figs. 2, 3, 7, 8, 11–14)

1929*a*. *Cryptolithus transiens* Bancroft, p. 90, pl. 2, fig. 5.
1933. *Broeggeria transiens* (Bancroft) Bancroft, table 1.
1945. *Broeggerolithus transiens* (Bancroft) Bancroft, pp. 196, 197.
1948. *Broeggerolithus transiens* (Bancroft) : Bancroft *in* Lamont, pp. 2, 5.
1949. *Broeggerolithus transiens* (Bancroft) : Bancroft, p. 298, pl. 9, fig. 8.
1958. *Broeggerolithus transiens* (Bancroft) : Dean, p. 208, pl. 26, fig. 11.

DESCRIPTION. Outline of the cephalon is usually well rounded, almost semicircular, though occasionally it may be slightly subangular anteriorly or anterolaterally. In front of the glabella the outline may appear slightly flattened owing to the narrowing of the fringe. The glabella is strongly convex, swollen anteriorly, and stands high above the tumid cheek-lobes from which it is separated by broad, fairly deep axial furrows containing small hypostomal pits situated well forwards. At the base of the glabella is a pair of small pits, and just behind these is another pair in the posterior half of the broad (*sag.*), shallow occipital furrow. The occipital ring is small, short and directed backwards and upwards, as is the small occipital spine into which it is produced. The pleuroccipital furrow is shallow, delimiting the narrow (*exsag.*) pleuroccipital segment which is transversely straight as far as the fulcral sockets, beyond which the posterior margin of the fringe runs outwards and rearwards to the genal angles, forming " ears " of moderate size. The junction of the occipital ring and the two halves of the pleuroccipital segment is marked by the presence of a pair of small apodemes. The genal spines extend rearwards more than the length of the cephalon, and are gently convex outwards ; they have a grooved upper surface, and a ridged lower surface.

The fringe is of even breadth, becoming slightly narrower in front of the glabella where four rows of pits are continuous. The surface of the upper lamella is generally flat, but small interradial ridges are developed anteriorly in the three outermost rows of pits. There is a slightly-raised concentric ridge between I_1 and I_2, and I_2 itself is depressed a little, especially anterolaterally. In front of the glabella all the pits are of equal size, but then, near the anterolateral angles, those of E_1 and I_{1-2} become much larger, though still of equal size, towards the genal angles. The marginal suture is of normal trinucleid type, but as it runs close to the pits of E_2 the marginal rim is extremely narrow. The mode and variation of the pits present are $E_1 + e_1 = 19$ (18–22) ; $E_2 + e_2 = 22$ (20–23) ; $I_1 + i_1 = 19$ (18–21) ; $I_2 + i_2 = 19$ (19–21) ; $I_3 + i_3 = 10$ (8–12) ; $I_4 + i_4 = 5$ (5–6). Pits along posterior margin of fringe $= 7$ (7–9). Pits external at genal angle $= 1$ (1–2).

As in *Broeggerolithus longiceps* the radii to the rear, and even just in front, of the anterolateral angles are flexed forwards at the I_{1-2} pseudogirder, and some auxiliary pits are present in E_2 in this portion of the fringe. The fringe of the holotype is incompletely preserved, but the notation in a topotype cephalon of comparable size, about 19 mm. wide, is $E_1 =$ 0–18, $E_2 =$ 0–18 ; $e_2 =$ xi, xii ; $I_1 =$ 0–17, $I_2 =$ 0–17, $I_3 =$ 12–17 ; $i_3 =$ xii, xiv, xvii. Internal to I_3 there is a triangular group of seven pits between the cheek-lobe and the posterior margin of the fringe.

The underside of the fringe shows an E_1–I_1 girder which is particularly strongly developed anteriorly, and a much smaller I_{1-2} pseudogirder which only appears posterolaterally. The line of the girder is continued as the longitudinal median ridge on the underside of the genal spine. A particularly conspicuous feature of the pitting is the manner in which the pits of E_{1-2} are situated in straight, shallow, radial sulci which diminish in depth away from the median line. In the most centrally positioned sulci the pits of E_{1-2} are close together, almost twinned, but beyond about R3 they are distinctly separate.

The thorax contains six segments of typical trinucleid form ; the third, fourth and fifth segments are equidimensional and the thoracic outline narrows forwards and rearwards from these. The narrowest part of the thorax is across the first, macropleural segment, the anterolateral edges of which run sharply backwards and outwards from the fulcral processes. Each pleura is divided into two bands of about equal size by a pleural furrow which runs outwards and slightly backwards from the axial furrow to the backwardly-directed pleural point. The axis is narrow, about one-quarter of the total breadth, and delimited by straight, shallow axial furrows. Each axial segment is curved forwards centrally and also laterally to form a pair of nodes just inwards from the axial furrows. On the inner side of each node a deep apodemal pit is situated in the deep, broad (*sag.*) articulating furrow.

The pygidium is triangular in outline, the breadth rather more than two-and-a-half times the length, with a steeply declined border and a bluntly-pointed tip. The axis is poorly defined, particularly posteriorly where it merges gradually with the pleural lobes, the inner parts of which are swollen at that point. There are five narrow (*sag.*) axial rings, between the first and second of which is sited a pair of small apodemal pits. The pleural lobes have not been found well preserved, but there appear to be only two furrows on each, and they are developed only in the slightly tumid outer portion.

HORIZONS AND LOCALITIES. The holotype was obtained from the middle portion of the Marshbrookian Stage, the *Dalmanella unguis* Beds or Zone, which forms the upper half of the quarry face in the small, disused quarry by the west side of the track through Marsh Wood, half a mile south of Marshbrook Station. The species occurs also in the lower half of the same quarry face, made up of the *Dalmanella wattsi* Beds, the lowest subdivision of the Marshbrookian. At both these horizons the species is not uncommon, and other localities include the south bank of the River Onny 160 yards east of the eastern end of Burrells Coppice, near Horderley; the edge of the field 340 yards north-west of Maplewall Cottage, near Woolston; the exposure 685 yards east-south-east of Cwm Head Farm; the lane-section about 400 yards south-south-east of Soudley Quarry, between Hope Bowdler and Ticklerton; and the stream-section 550 yards south-south-west of Common Farm, Wallsbank. According to Bancroft (1929*a* : 91) *B. transiens* is found only in the middle subdivision of the Marshbrookian, but it is now known from both the lowest and highest beds. In the uppermost third of the Stage, known variously as the *Onniella reuschi* or *Kjerulfina polycyma* Zone, it is found much less abundantly than at lower horizons. Localities at this level include the west side of the track just south of Marsh Wood Quarry (see above); the west side of the road 20 yards west-north-west of Maplewall Cottage, near Woolston; and by the south bank of the River Onny 1050 yards west-south-west of Wistanstow Church. *B. transiens* is characteristic of the Marshbrookian Stage in south Shropshire, and outside the county has been recorded only from the Cross Fell Inlier, apparently at the same general horizon. This paucity of occurrences is probably the result of the general absence of Marshbrookian strata.

HOLOTYPE. BM. In. 42071.

FIGURED SPECIMENS. BM. In. 49129 (Pl. 18, figs. 12, 13); BM. In. 50594 (Pl. 18, fig. 7): BM. In. 50602 (Pl. 18, fig. 14); BM. In. 50604 (Pl. 18, fig. 8); BM. In. 52050 (Pl. 18, fig. 3); BM. In. 54001 (Pl. 18, figs. 2, 11).

DISCUSSION. Of all the other Shropshire trinucleids *B. transiens* bears most resemblance to *B. longiceps*, with which it shares a similar fringe form and pitting, together with the frequent persistence of coarse reticulation on the cheek-lobes of numerous adult specimens. The glabella of *B. transiens* is, however, usually shorter and more swollen anteriorly, and the pit-count for a mature cephalon is much smaller. Both species have a similar number of auxiliary pits in E_2, but whereas those of *B. transiens* are situated anterolaterally, those of *B. longiceps* are much closer to the genal angle. On the underside of the fringe of *B. transiens* the presence of closely-set pits of E_{1-2} in radial sulci is a feature not yet seen in mature cephala of the Upper Longvillian species, though a suggestion of it has been found in an immature specimen.

Broeggerolithus cf. ***transiens*** (Bancroft)

(Pl. 18, fig. 9)

The Bancroft Collection at the British Museum (Natural History) contains a small number of specimens from a temporary excavation, a well digging, made in the Marshbrookian strata of the Wistanstow district. They include three mature cephala belonging to *Broeggerolithus*, the largest having a maximum breadth of 21 mm. The form represented appears to agree closely with *Broeggerolithus transiens* (Bancroft) but small differences between the two are found ; these include a slightly larger pit-count than the *forma typica*, a smaller number of pits in E_2, a general lack of auxiliary pits in E_2 and I_3, and a larger number of small pits in the area of the fringe internal to I_3. One specimen, BM. In. 52823, 20 mm. broad, possesses a twinned pair of pits in E_{1-2} near the left anterolateral angle, and has the fringe notation : E_1 0–20, E_2 0–19 ; e_1 xviii ; I_1 0–20, I_2 0–18, I_3 11–19, I_4 16–19 ; i_1 xx, i_3 xix, i_4 xv, xix. I_5 consists of three small pits rather irregularly arranged.

The best-preserved cephalon shows coarse reticulation on the surface of the glabella, but it is not clear whether this persists on the cheek-lobes. The species may prove to be specifically distinct from *B. transiens*, but in view of the limited material available it seems more advisable to compare it with that form.

Horizon and locality. The label attached to the specimens by Bancroft described them as coming from a " well-digging at the first house along the road south from The Corner ". The Corner is a hamlet situated about one and a quarter miles almost due north of Wistanstow Church, and the road referred to runs from the western end of the hamlet towards Wistanstow. The date of Bancroft's label is unknown, and it does not state from which side of the road his specimens originated, but it may be noted that the 6-inch Ordnance Survey map indicates a well by the west side of the road 200 yards south-south-east of the right-angle in the road which gives The Corner its name. The map does not show any other well along this stretch of road. The rock itself is a yellowish-grey, hard, calcareous mudstone and the associated fauna includes *Kjerulfina polycyma* Bancroft, indicating the *Onniella reuschi* Zone, the topmost subdivision of the Marshbrookian Stage. No surface exposures of rock have been found at The Corner itself, but field-mapping of the area by the writer confirms that rocks of high Marshbrookian age are, in fact, present underneath the hamlet.

Figured specimen. BM. In. 52823.

Genus ***ONNIA*** Bancroft, 1933

Bancroft's original diagnosis of the genus was brief and unsatisfactory, stating merely that *Onnia* "differs from the other genera of the subfamily in having the external spine-channel continuous with E_2, in the large number of pits in that row and their regularly concentric arrangement. I_4 is always present on the side of the cheek" (1933 : 2). Whittard (1958 : 88, 89), in discussing the genus *Broeggerolithus*, has suggested that it might be congeneric with *Onnia* on account of the two having in common a superficially similar fringe with two continuous rows of pits external to the girder, the differences between the two genera being confined to what he considers unimportant features. The present study of Caradoc trinucleids tends to confirm Bancroft's separation of *Onnia* from *Broeggerolithus*, and an attempt is made below to enumerate the features found most constant and useful in distinguishing the two.

Onnia	*Broeggerolithus*
E_1 and I_1 consist of pits mostly of equal size and larger than those of adjacent rows.	Only one row of larger pits, E_1 in Group 2, and I_1 in Group 3.
E_1 and I_1 are raised above neighbouring rows.	In Group 2, E_1 is raised, but the fringe is flat in the other groups.
Radial arrangement is strong, but no interradial ridges developed.	Group 2 has strongly developed interradial ridges, which are found on a smaller scale in Gp. 3, but not in Gp. 1.
Radii straight, found almost as far as the genal angles, and never flexed forwards.	Radii frequently flexed strongly at the line of the I_{1-2} pseudogirder.
Auxiliary pits numerous and regular in all parts of E_2.	Auxiliary pits never numerous, and usually restricted to one limited part of the fringe, except in *B. harnagensis*, when they are often irregularly arranged out of concentric line.
E_2 always complete anteriorly, and only rarely is a pit absent at the genal angle.	Several pits may be absent from E_2, both anteriorly and at the genal angle.
I_3 and I_4 are well developed, extending from as far forwards as R3 and R8 respectively.	I_3 not known farther forwards than R10, and I_4 usually consists only of a few pits.
Several pits of I_{2-4} are set in radial sulci.	Radial sulci rarely developed.
Genal spines long, more or less continuous with the lateral margins.	Genal spines short or of moderate length, often markedly splayed at an angle to the lateral margins.

In addition it may also be noted that in *Onnia* the " ears " of the fringe are always large, whilst in *Broeggerolithus* (*s.s.*) they are typically small, though becoming larger in species of Group 3, the stratigraphically younger forms.

Distribution. The appearance of *Onnia*? *cobboldi* (Bancroft) is used to define the base of the Onnian Stage, or *Onnia* Beds, in south Shropshire where the genus ranges upwards throughout the Stage. The horizontal distribution of *Onnia* throughout the Caradoc Area cannot be assessed owing to lack of outcrops. Two of the species usually assigned to the genus, *O. gracilis* and *O. superba*, are known also from the Cross Fell Inlier, and *O. gracilis* is found at Welshpool. Extra-British occurrences include *O. ornata* (Sternberg) in Bohemia and Portugal, and *O. cobboldi* has been reported from North Africa (G. & H. Termier, 1950 : 22). Another form possibly referable to *Onnia* comes from southern Norway. An alleged member of the genus has been figured from Venezuela as *O. terryi* (Leith) by Whittington (1954), but this identification cannot be upheld and the writer agrees with Whittard's view (1958 : 89) that the species is probably best placed in *Salterolithus*, at least for the time being, though a new generic name may eventually prove necessary. Another record of *Onnia* from South America (Rusconi, 1956 : 9) is also thought to be incorrect.

It has been found more convenient to group together the discussions of the various Shropshire Onniae at the end of this chapter, after the account of *Onnia superba*.

TYPE SPECIES. *Cryptolithus superbus* Bancroft, 1929, by original designation of Bancroft (1933 : 2).

Onnia? cobboldi (Bancroft)

(Pl. 19, figs. 1, 3, 12)

1929*a*. *Cryptolithus cobboldi* Bancroft, p. 92, pl. 2, figs. 6, 7.
1933. *Onnia cobboldi* (Bancroft) Bancroft, table 1.
1940. *Onnia cobboldi* (Bancroft) : Whittington, p. 245.
1948. *Onnia cobboldi* (Bancroft) : Lamont, p. 418, pl. 1, figs. 6–8.
1949. *Onnia cobboldi* (Bancroft) : Bancroft, p. 299, pl. 9, figs. 10, 11.
1958. *Onnia cobboldi* (Bancroft) : Dean, pl. 26, fig. 14.

DESCRIPTION. The cephalic outline is well rounded in front, forming more than half a circle, the posterolateral margins converging forwards from the bases of the genal spines which are situated at the extremities of moderately large " ears ". The greatest breadth occurs across the genal angles and is about equal to the total length of the complete exoskeleton, and almost twice the median length of the cephalon. The glabella is pear-shaped, swollen anteriorly, and stands high above the cheek-lobes, culminating in a median ocellus situated at its apex. In some specimens where the shell material is slightly translucent three pairs of dark muscle-scars show through ; the first of these comprises large scars, but the others decrease in size rearwards, and the third pair almost coincides laterally with a pair of shallow pits situated just inside the axial furrows and in front of the occipital furrow. The axial furrows are broad and shallow, with small hypostomal pits situated well forwards, and only slightly convex outwards, bordering moderately swollen cheek-lobes. The occipital furrow is shallow medially but deepens laterally where a pair of occipital pits is sited ; the occipital ring is short, produced upwards and backwards into a slim occipital spine. The pleuroccipital furrow and segment are narrow (*exsag.*), the former only moderately deep, and extend to the fulcral sockets which are situated less than halfway from the axial furrows to the lateral margin. Beyond the fulcral sockets the posterior margins of the fringe are straight, directed slightly rearwards to the genal angles so as to enclose " ears " of moderate size. The genal spines, which are at least slightly longer than the cephalon (*sag.*), are not quite continuous with the lateral margins of the cephalon ; each carries a longitudinal groove on its upper surface, a longitudinal ridge on its lower surface and becomes slightly incurved towards the tip. The marginal suture, of normal trinucleid type, runs just below the top of the moderately declined border and clearly demarcates the smooth surface of the upper lamella from that of the lower lamella which, together with its genal spine, carries well-defined, closely grouped terrace-lines.

The fringe is of moderate width with three continuous rows of pits E_{1-2} and I_1, narrowing slightly in front of the glabella, the encroachment of which is accommodated by the absence of a few pits, generally four, of I_2. E_1 and I_1 consist of larger, usually more polygonal pits than the other rows, and both of them, though generally more particularly E_2, are slightly raised above the level of the rest of the upper lamella. E_2 contains slightly smaller pits, together with a few auxiliary pits distributed fairly uniformly. I_3 and I_4 are well developed, though occasional pits are completely absent from the latter row. In cephala of young individuals radial sulci are found which contain pits of I_{1-4}, but in the adult and in a cephalon 10 mm. wide, the pits of I_1 are larger and bordered on their inner side by a concentric I_{1-2} ridge separating them from the radial sulci which now include only pits of I_{2-4}. The number of pits present in the adult trilobite is $E_2 = 18–24$ (mode = 22), $E_1 = 18–21$ (mode = 19), $I_1 = 18–22$ (mode = 19), $I_2 = 16–19$ (mode = 17), $I_3 = 13–16$ (mode = 14). Fewer specimens with well-preserved I_4 have been found, but apparently the usual number of pits present is 10. These figures are based on material from the type-locality. The holotype itself is insufficiently preserved for its fringe notation to be written in full, but for a typical large adult specimen, BM. In. 49026, 25 mm. wide and 10·5 mm. long medially, it is E_1 1–19, E_2 1–18 ; e_2 0, iii, viii, xiv ; I_1 1–18, I_2 3–19, I_3 8–17, I_4 10–12, 15, 16, 18 ; i_1 xvii, i_2 xvii, i_3 xiii, xvii. The underside of the fringe carries a girder which is only moderately developed, and an I_{1-2} pseudogirder which is poorly defined.

The thorax contains six typically trinucleid segments, the first of them macropleural ; the third and fourth segments are the widest (*tr.*), the outline of the thorax then narrowing slightly towards both cephalon and pygidium. The axis occupies about one-quarter of the total breadth, is bounded by poorly-defined axial furrows, and is not markedly convex above the side-lobes. Each pleura is smooth apart from a pleural furrow which commences at the front edge coincident with the axial furrow and runs straight outwards and slightly backwards to the backwardly-directed, slightly turned-down pleural point. The pleura is thus divided into two bands, of which the posterior is the larger.

The pygidium is roughly triangular in plan, the length being about one-third of the maximum breadth, which is also approximately equal to the length of the cephalon. Frontally the triangular axis occupies one-quarter of the breadth, is delimited by very shallow axial furrows, and merges gradually with the side-lobes. Each axial ring possesses two pairs of muscle-scars which show through the test as small dark patches ; the inner pair is situated slightly in front of the outer pair which is located almost on the lines of the axial furrows. Only six axial rings have been seen, but there are eight sets of muscle-scars, extending almost to the tip of the axis. Each side-lobe has a small raised marginal rim and usually five pleural furrows which decrease in depth from first to last ; the pleurae so formed are continuous with their corresponding axial rings. The pygidial border is steeply declined, becoming shallower towards the tip, and covered with closely-crowded terrace-lines parallel to the marginal rim.

Horizon and localities. The type-locality is in the bed of the River Onny by the south bank, about 45 yards east-south-east of the point where Batch Gutter joins the river. The species occurs also at various other points in the vicinity of the type-locality, particularly the north bank of the Onny 63 yards east-south-east of its junction with Batch Gutter, and is found throughout a thickness of about forty feet of rock. *Onnia*? *cobboldi* marks the lowest subdivision, the zone to which it gives its name, of the Onnian Stage, and is accompanied by abundant *Onniella inconstans* Bancroft with occasional *Platylichas* and *Chasmops*. Owing to the lack of exposures the species is not encountered in south Shropshire outside the Onny Valley and has not yet been found elsewhere in Britain.

Lectotype, here selected. BM. In. 42072, a cephalon figured by Bancroft (1929*a*, pl. 2, fig. 6).

Paratype. Bancroft's other syntype (1929*a*, pl. 2, fig. 7), a pygidium, has not yet been traced.

Figured specimens. BM. In. 49026 (Pl. 19, figs. 3, 12) ; BM. In. 49028 (Pl. 19, fig. 1).

Onnia gracilis (Bancroft)

(Pl. 19, figs. 2, 7)

1929*a*. *Cryptolithus gracilis* Bancroft, p. 94, pl. 2, figs. 8, 9.
1933. *Onnia gracilis* (Bancroft) Bancroft, table 1.
1938. *Cryptolithus gracilis* Bancroft : Shackleton, p. 455.
1940. *Onnia gracilis* (Bancroft) : Whittington, p. 245.
1948. *Onnia gracilis* (Bancroft) : Lamont, p. 418, pl. 1, fig. 9.
1949. *Onnia gracilis* (Bancroft) : Bancroft, p. 299, pl. 9, fig. 9.
1958. *Onnia gracilis* (Bancroft) : Dean, p. 212, pl. 26, fig. 15.

Description. The cephalic outline is generally well rounded, nearly a semicircle, often slightly subangular frontally. The glabella is roughly pear-shaped, swollen anteriorly, stands moderately high above the cheek-lobes, and has a distinct median ocellus. Basal glabellar furrows are represented by a pair of small apodemal pits, in front of which two pairs of flattened ovoid impressions or muscle-scars may be seen in well-preserved specimens. The axial furrows are deep, broad, gently convex outwards, and contain hypostomal pits of moderate size near their anterior ends. Numerous cephala with the test intact have been examined, but none shows the group of large punctae immediately in front of each hypostomal pit such as is described elsewhere in this paper from *Onnia superba* and *Broeggerolithus harnagensis*?. The axial furrows border convex cheek-lobes, the surface of which is smooth in the adult trilobite but reticulate in immature cephala at least up to about 8 mm. wide.

The occipital furrow is broad (*sag.*) and shallow, with a pair of deep occipital pits near its outer ends, and the small occipital ring is produced backwards and upwards to form a short occipital spine. The pleuroccipital furrow is shallow and fairly broad (*exsag.*) ; both it and the narrow (*exsag.*) pleuroccipital segment follow a gently sigmoidal course to the fulcral sockets, situated just less than half-way from the axial furrows to the lateral margins. Beyond the fulcral sockets the posterior margins of the fringe are convex rearwards, directed outwards and backwards to the genal spines so as to form large " ears ". The genal spines are continuously in line with the lateral margins of the fringe and irregularly quadrilateral in cross-section, each of the four sides having a longitudinal groove developed to a varying degree. The attitude of the cross-section is such that one of the grooved sides is uppermost, continuous with the surface of the upper lamella, whilst one of the ridges runs longitudinally along the underside of the spine continuous with the girder.

The cephalic fringe is broad, becoming narrower in front of the glabella where four rows of pits, E_{1-2} and I_{1-2}, are continuous, and markedly broader posterolaterally where it expands rapidly behind the cheek-lobes. Frontally the pits of all the four rows present are of similar size except those of E_1, which are much larger, but laterally the pits of I_1 expand to the same large size whilst those of the other rows remain small. Both E_1 and I_1, particularly the former, are raised slightly above the level of the other rows. E_2 extends to the genal angle and consists of very small pits, numerous and crowded together so that the strong radial arrangement which extends outwards from I_4 to E_1 inclusive is only poorly developed. I_3 and I_4 are both well developed, extending from as far forwards as R3 or R4 and R10 or R11 respectively. The pits of I_{2-4} are set in slightly depressed radial sulci over the anterolateral and lateral portions of the fringe, but these, together with the marked radial arrangement of fringe pits in general, extend usually only as far as about R20, beyond which point there is a more random arrangement of pits near the posterior margin. The number of pits present in each of the concentric rows is as follows, the figure in brackets representing the mode. $E_2 + e_2 = 31–37$ (34), $E_1 + e_1 = 21–25$ (22), $I_1 + i_1 = 21–25$ (22), $I_2 + i_2 = 21–25$ (23), $I_3 + i_3 = 17–23$ (20), $I_4 + i_4 = 13–18$ (16).

The pits along the posterior margin of the fringe number from 8–11, though more commonly 9. The fringe notation for the lectotype cephalon is E_1 0–22, E_2 0–22 ; e_1 xxi, xxii, e_2 0, ii, iii, vi, viii, xi, xiii, xv, xvii, xx, xxii ; I_1 0–22, I_2 0–22, I_3 4–22 ; I_1 xxi, i_2 xxi, xxii, i_3 xxi, xxii ; $I_4 + i_4$ consists of about 17 pits, radially arranged from R10 to R20 but then becoming irregularly disposed ; $I_5 + i_5$ consists of 5 pits irregularly arranged, but forming a well-defined line at and behind the posterolateral part of the cheek-lobe.

On the lower lamella of the fringe is a poorly-marked girder together with two pseudogirders situated I_{1-2} and E_{1-2}. All these concentric ridges are developed to about the same degree, and the girder appears to coalesce with the outer pseudogirder near the genal angle just before running into the longitudinal ridge of the genal spine. The I_{1-2} pseudogirder extends only to the more random group of pits beyond about R20 mentioned earlier and does not attain the posterior margin of the fringe. Each girder or pseudogirder carries a narrow band of three or four terrace-lines along its length. Closely-grouped terrace-lines are found also on that portion of the moderately-declined cephalic border below the line of the marginal suture. The cephalon of the paratype, a whole individual (Pl. 19, fig. 7), has apparently been damaged during the life-time of the animal and subsequently healed. The upper lamella is broken off diagonally near the genal angle, so that E_1 extends only as far as R18. The damaged portion of the fringe is not quite complete, but the posterior margin appears to have regenerated along the broken edge, and there is now no sign of the course of the marginal suture which normally cuts the posterior margin at roughly its mid-point.

The thorax contains six thoracic segments, the first of which is macropleural. The greatest breadth occurs across the third, fourth and fifth segments, to the front and rear of which the outline narrows slightly. The thoracic axis is narrow, about one-fifth of the total breadth, stands moderately high above the side-lobes, and is bounded by broad, shallow, poorly-defined axial furrows. In addition to the articulating furrow each segment carries a median transverse furrow on the axial ring, moderately deep at the axial furrows but almost obsolete medially. Each pleura has a strong pleural furrow which commences at the intersection of the anterior margin and the inner boundary of the axial furrow, and then runs outwards and backwards towards the pleural tip which ends posterolaterally in a backwardly-directed point. The pleural furrow becomes deeper and broader (*exsag.*) outwards, and divides the pleura into two bands, of which the anterior is the smaller.

The pygidium is subtriangular in outline, roughly three times as broad as long, with a narrow, well-defined, convex axis occupying rather less than one-sixth of the frontal breadth and extending to the tip of the pygidium. Axial rings are numerous, usually about nine, with two pairs of small, dark muscle-scars situated in each axial furrow. The side-lobes each have seven or eight pleurae, becoming less well defined rearwards, the first two or three of which carry traces of rib furrows. The steeply-declined border is ornamented with terrace-lines and topped by a raised marginal rim.

HORIZON AND LOCALITIES. The type-specimens are from the ledge-like bed of calcareous grey mudstone running north-north-east across the River Onny 100 yards east of the junction of the river and Batch Gutter, south-west of Wistanstow. The species is abundant there, but occurs both above and below this level throughout a thickness of about 60 feet of rock marking a zone within the Onnian Stage or *Onnia* Beds. No other occurrences of the species are known from south Shropshire, but *Onnia gracilis* is abundant in the Cross Fell Inlier and is known from the Gwern-y-brain Shales of Welshpool.

LECTOTYPE, here selected. BM. In. 42074 (Pl. 19, fig. 2). An incomplete cephalon with the test preserved, figured previously by Bancroft (1929*a*, pl. 2, fig. 8) and Dean (1958, pl. 26, fig. 15).

PARATYPE. One of the syntypes figured by Bancroft (1929*a*, pl. 2, fig. 9) showed merely a pygidium, not quite complete, with a fragment of some thoracic segments close by. It is now plain that the figure in question showed only a portion of a whole individual, BM. In. 49032, which is here figured in its entirety (Pl. 19, fig. 7).

Onnia superba (Bancroft)

(Pl. 19, figs. 4–6, 8, 9, 11, 13, 14)

1839. *Trinucleus caractaci* Murchison, pl. 23, figs. 1 d–f only.
1854. *Trinucleus concentricus* Eaton : Murchison, pl. 4, fig. 3 only.
1859. *Trinucleus concentricus* Eaton : Murchison, pl. 4, fig. 3 only.
1867. *Trinucleus concentricus* Eaton : Murchison, pl. 4, fig. 3 only.
1872. *Trinucleus concentricus* Eaton : Murchison, pl. 4, fig. 3 only.
1884. *Trinucleus concentricus* (Eaton) : La Touche, pl. 3, fig. 55.
1912. *Trinucleus concentricus* (Eaton) : Reed, pp. 347, 349, 351, pl. 18, figs. 1, 4, 7, 12.
1912*a*. *Trinucleus concentricus* (Eaton) : Reed, p. 387.
1914. *Trinucleus concentricus* (Eaton) : Reed, p. 355, pl. 29, figs. 3, 3a.
1929*a*. *Cryptolithus superbus* Bancroft, p. 95, pl. 2, fig. 10.
1933. *Onnia superba* (Bancroft) Bancroft, p. 2, table 1.
1940. *Onnia superbus* (Bancroft) : Whittington, p. 245.
1948. *Onnia superba* (Bancroft) : Lamont, p. 418, pl. 1, figs. 1–5.
1949. *Onnia superba* (Bancroft) : Bancroft, p. 299, pl. 9, fig. 12 ; pl. 10, fig. 16.
1958. *Onnia superba* (Bancroft) : Whittard, p. 88.
1958. *Onnia superba* (Bancroft) : Dean, p. 212, pl. 26, fig. 16.

DESCRIPTION. The cephalic outline is usually subangular both frontally and anterolaterally, the maximum breadth being slightly more than twice the median length, excluding the occipital spine. The glabella is high, swollen anteriorly and generally rather narrow, though this often appears exaggerated owing to crushing ; it encroaches on the fringe and is accommodated by the flexing forwards of E_1 and I_1, and the absence of a few pits of I_2. Glabellar furrows are represented only by one pair of small, basal apodemal pits. The cheek-lobes are smooth, quadrant-shaped, moderately convex, and separated from the glabella by fairly deep, gently curved axial furrows. Each furrow has a deep hypostomal pit situated well forwards, and between this and the pits of the cephalic fringe there have been found, in a few better-preserved specimens, all of them internal moulds with a limonitic replacement of the test, a series of small punctae which are just visible under a hand lens. These, the function of which is not yet apparent (but see p. 106), begin just outside the line of the hypostomal pit and extend inwards covering a small rectangular area about 1 mm. long (*tr.*) ; in one or two of the specimens there appear to be about six or seven rows, each with three punctae. The occipital furrow is only moderately deep medially, becoming still shallower laterally where a pair of occipital pits is sited, marking the small occipital ring which is directed backwards and upwards, and produced to form a small occipital spine. The shallow pleuroccipital furrow and narrow (*exsag.*) pleuroccipital segment run straight out from the axial furrows to the fulcral sockets, about halfway to the lateral margins ; beyond the fulcral sockets the posterior margins of the fringe turn back sharply towards the bases of the genal spines, so as to form large " ears ". The genal spines are long, the longest known being almost three times the median length of the cephalon, and continue along the lines of the lateral margins of the cephalon. The upper surface of each spine is longitudinally grooved, the underside has a median ridge continuous with the girder, and the tip is gently incurved.

The cephalic fringe is wide posterolaterally, narrowing in front of the glabella where only the three outermost rows of pits, E_{1-2} and I_1, are complete. The marginal suture is of the usual trinucleid type and there is a small, raised marginal rim. The pits of E_1 and I_1 are noticeably larger and more polygonal than those of adjacent rows, and become still larger posterolaterally; the two rows are raised above the surface of the remainder of the upper lamella. A concentric ridge is developed between E_1 and I_1, and the raised portion of the upper lamella is separated from the rest by similar ridges situated E_{1-2} and I_{1-2}. The outermost row, E_2, is conspicuous on account of the smallness of its pits and the presence of several auxiliary pits distributed along its entire length, which extends to the genal angle. The area internal to the ridge separating I_1 and I_2 is particularly noteworthy for the development there of interradial ridges, lower than E_1 and I_1, between which the pits of I_{2-4} are sunk in radial sulci; the interradial ridges commence about R7 or R8 and extend as far as about R15 or R16. The number of pits present in each of the four outermost concentric rows is $E_2 + e_2 = 25–28$ (mode = 27 or 28), $E_1 + e_1 = 16–19$ (mode = 18), $I_1 + i_1 = 18–21$ (mode = 19), $I_2 + i_2 = 16–20$ (mode = 17). The fringe of the holotype is not completely preserved, so that it is impossible to write the pit notation, but a typical large adult specimen, BM. In. 52089, 23 mm. wide, exhibits the following pattern E_1 1–18, E_2 1–18; e_2 0, vii, ix, xiii, xv, xvii; I_1 1–18, I_2 3–18, I_3 7–18, I_4 13–18; i_1 xv, i_2 xv, xvii, i_3 xv, xvi, xviii, I_4 xv, xvi, xvii. The number of pits along the posterior margin of the fringe is usually seven or eight. The ventral surface of the fringe possesses a well-developed girder which follows the bluntly angular outline of the cephalon frontally and diminishes considerably beyond the anterolateral angles. An I_{1-2} pseudogirder is also found, but is only significant laterally and posterolaterally.

The thorax consists of six typically trinucleid segments, the first macropleural. The thoracic axis, roughly one-quarter of the total breadth, is bounded by shallow, almost straight, subparallel axial furrows. The internal mould of each axial ring carries a moderately deep articulating furrow, at either end of which, just inside the axial furrow and bordering a small axial node, is a deep apodemal pit. Each pleura is flat, divided into two bands by a pleural furrow which commences at the anterior edge just outside the axial furrow and runs outwards and backwards to the blunt, backwardly-directed pleural point, in the vicinity of which it becomes slightly deeper.

The pygidium is subtriangular in outline, with a border steeply declined over most of its length, becoming less so at and near the bluntly-pointed posterior termination. Frontally the axis occupies about one-fifth of the maximum breadth; it is triangular in plan, bounded by shallow axial furrows, stands moderately high above the pleural lobes, and extends to the tip of the pygidium. The first axial furrow is marked laterally by a pair of small, slot-like apodemal pits, but thence to the posterior tip of the axis there are several axial rings, usually up to eight or nine, which are poorly defined. The pleural lobes are flat, bounded by a small, bevelled, raised rim, and each carries a series of pleural furrows continuous with the ring furrows. The pleural furrows are badly defined on the internal mould, becoming less distinct towards the tip of the pygidium, and even on the external mould only the first two pairs of furrows are at all clearly marked.

IMMATURE INDIVIDUALS. The mudstones at the type-locality of *Onnia superba* have yielded several specimens of the young of the species. Unfortunately their presence as disarticulated cephala makes it impossible for the various degrees of development to be worked out in detail, nevertheless, something can be learned of the successive changes in the form of the cephalon.

The smallest cephalon available, BM. In. 50701, is 2·5 mm. wide and about 1·0 mm. long. Its preservation is poor, but it shows three rows of pits in front of the glabella, and a pair of short (*tr.*) ocular ridges which run outwards and slightly backwards from the glabella just in front of its midpoint, crossing the axial furrows. The characteristics of larger cephala are enumerated in semi-tabular form below.

Cephalic Length (mm.)	Cephalic Breadth (mm.)	Characteristics
1·25–1·5	3·5–3·75	E_{1-2} complete, I_1 almost complete. Cheek lobes reticulate. Ocular ridges and median ocellus present. Alar lobes developed, about half the length of the glabella, triangular in form, bounded on the outside by the axial furrows, on the inside by the shallow alar furrows, and posteriorly by the occipital furrow.
1·8	4·0	Ocular ridges less well developed. Alae slightly smaller and narrower. I_2 developed as far forwards as R3. Pits present : $E_2 + e_2 = 23$, $E_1 + e_1 = 18$, $I_1 + i_1 = 19$, $I_2 + i_2 = 16$.
2·0	5·0	Reticulate cheek-lobes. Ocular ridges poorly developed. Alae shorter and more rounded. Occipital spine more conspicuous. Pits of E_1 and I_1 noticeably larger. Traces of radial sulci in I_{2-3}. I_2 from between R2 and R5, I_3 from R7. $E_2 + e_2 =$ 23–27 pits, $E_1 + e_1 =$ 19–20, $I_1 + i_1 =$ 18–19, and $I_2 + i_2 =$ 15–18.
2·3–2·5	5·5–6·0	Cheek-lobes reticulate. No ocular ridges seen. Median ocellus present. Alae are indistinct swellings, poorly defined. $E_2 + e_2 = 24$ pits, $E_1 + e_1 = 18$, $I_1 + i_1 =$ 17–19, $I_2 + i_2 =$ 17–18. I_2 developed from R3, and I_3 from R5 or R7.
3·8–4·0	8·0–8·5	Median ocellus present. One specimen with strong occipital spine half the length of the glabella. Cheek-lobes reticulate. $E_2 + e_2 =$ 22–23 pits, $E_1 + e_1 = 18$, $I_1 + i_1 = 18$, $I_2 + i_2 =$ 16–19, I_2 developed from about R2, I_3 from R7, and I_4 from R12. Alae not developed.
4·0	9·5	Cheek-lobes reticulate. Number of pits present much the same as in previous group, with one or two more in E_2.
5·5	12·0	Cheek-lobes reticulate. E_1 and I_1 comprise larger pits and raised above adjacent rows. $E_2 + e_2 = 28$ pits, $E_1 + e_1 = 20$, $I_1 + i_1 = 20$, $I_2 + i_2 = 21$.
6·0	13·0	Reticulation of cheek-lobes less pronounced. Six thoracic segments present, and this is the youngest holaspid known with certainty. The general appearance, and number of pits present in the four outermost rows much the same as in larger adults. $E_2 + e_2 = 27$ pits, $E_1 + e_1 = 19$, $I_1 + i_1 = 20$, $I_2 + i_2 = 16$. I_3 developed from R7, I_4 from R11, and radial sulci found in I_{2-4}.

Horizon and locality. The type-locality is the small cliff formed by yellow-weathering mudstones in the north bank of the River Onny 160 yards east of the junction of the river and Batch Gutter, and 720 yards west-south-west of Wistanstow Church. The place has been known to many generations of geologists as " The Onny Section ", and has been the source of almost all the specimens of *Onnia superba* collected from Shropshire. The species occurs there in great profusion, and entire adult individuals are by no means rare. *O. superba* occurs throughout a thickness of about fifty feet of rock, including strata, found only in the river bed, below and above those exposed in the main cliff section, and marks the topmost subdivision or zone of the Onnian Stage. Elsewhere the species has only been recorded from the Cross Fell Inlier.

Holotype. BM. In. 42070, a nearly complete cephalon preserved as an internal mould.

Figured specimens. BM. In. 42070 (Pl. 19, fig. 9) ; BM. In. 49029 (Pl. 19, figs. 13, 14) ; BM. In. 49030 (Pl. 19, fig. 11) ; BM. In. 49157 (Pl. 19, fig. 6) ; BM. In. 49158 (Pl. 19, figs. 4, 5) ; BM. In. 50709 (Pl. 19, fig. 8).

Onnia aff. ***superba*** (Bancroft)

(Pl. 19, fig. 10)

In association with the extremely abundant specimens of *Onnia gracilis* found at the type-locality of that species there occurs rarely another form of *Onnia* which bears a general resemblance to *Onnia superba* and is probably related to it.

The cephalic outline is fairly well rounded frontally and slightly subangular anterolaterally. The glabella is slightly clavate anteriorly, has a small median ocellus, and stands high above the only moderately convex cheek-lobes ; through the translucent calcite of the test can be seen three pairs of dark muscle-scars, the first and third pairs small, the second pair much larger, and between the basal pair of scars and the occipital furrow is a pair of very small apodemal pits. The axial furrows are almost straight, broad, and moderately deep. The occipital furrow is shallow and poorly defined, and the small occipital ring is produced to form a small occipital spine. The pleuroccipital furrow and segment are both narrow (*exsag.*) and gently sigmoidal as far as the fulcral sockets which are situated less than halfway from the axial furrows to the lateral margins. The fringe is fairly broad posterolaterally, but narrows frontally where only three concentric rows of pits are continuous in front of the glabella. The pits of E_1 are larger than those of the other rows except posterolaterally, where the pits of I_1 attain a comparable size. E_1 and I_1 are both separated and delimited by slightly raised concentric ridges, and the portion of the fringe occupied by both rows is elevated above the remainder of the fringe. E_2 consists of numerous small pits and extends to the genal angle, whilst the pits of I_{2-4}, also small, are set in radial sulci posterolaterally. The fringe notation for the figured, and best-preserved, specimen is E_1 1–21, E_2 1–21 ; e_2 0, iii, x, xv, xvii, xix, xxi ; I_1 1–21, I_2 4–21, I_3 8–16, 18–22, I_4 13–22. There is a triangular group of pits between I_1 and I_2 at the posterior margin of the fringe, and there are eight pits situated along the posterior margin of the fringe.

The thorax and pygidium are unknown.

HORIZON AND LOCALITY. The north bank of the River Onny 100 yards east of the junction of Batch Gutter with the river. The exposure is at the northern end of the outcrop in the bed of the Onny which yielded the type-specimens of *Onnia gracilis*, and is at the same horizon.

FIGURED SPECIMEN. BM. In. 54037 (Pl. 19, fig. 10).

DISCUSSION. For the sake of convenience the various species assigned to *Onnia* in south Shropshire are discussed together here instead of individually.

The earliest form, *Onnia*? *cobboldi*, is only tentatively referred to *Onnia* as it exhibits certain features which are not typical of the genus in its restricted sense and which distinguish it from other Onniae, namely, a relatively long cephalon and general lack of auxiliary pits in E_2. Some individuals, though not all, do not have E_1 and I_1 elevated above the remainder of the upper lamella of the fringe. Such features are more characteristic of *Broeggerolithus*, especially in its stratigraphically later species, but against them must be set the possession of other features which are typical of *Onnia* (*s.s.*), viz. I_3 and I_4 are strongly developed, from R8 and R10 respectively, E_2 extends to the genal angle and I_2 is discontinuous in front of the glabella, as in the type-species of *Onnia*. The balance is therefore on the side of retaining the species *cobboldi* in *Onnia*, though with reservations. It is the first trinucleid found in south Shropshire after a long interval, represented stratigraphically by the Actonian Stage, in the otherwise fairly constant line of development within the group and when this gap in our knowledge has been filled it seems quite likely that *O.*? *cobboldi* may be found to be intermediate between the later members of *Broeggerolithus*, themselves somewhat transitional, and *Onnia* of the *superba* group. G. & H. Termier (1950, pl. 187, figs. 8–11) have figured what they call *Onnia cobboldi* from the Caradoc of Morocco, but, judging from their inadequate illustrations, the identification must be regarded as suspect.

Onnia gracilis, though occurring abundantly throughout the middle portion of the Onnian Stage, differs in several obvious respects from the other Shropshire Onniae. The cephalon of *Onnia gracilis* is proportionately much wider and shorter, E_2 consists of a large number of small pits, including numerous auxiliary pits, E_1 is usually more elevated than I_1 above the rest of the upper lamella, and I_2 is continuous in front of the glabella, a characteristic not seen in *O.*? *cobboldi* or *O. superba*. The Bohemian species *Onnia ornata* (Sternberg) shares all these features with *O. gracilis*, but differs in possessing a generally smaller number of fringe pits, and a cephalic outline in which the lateral margins of the adult trilobite are parallel or divergent forwards. The alar lobes of young individuals of *O. ornata* described by Whittington (1940) are not crossed by the occipital furrow, unlike those of *O. superba* in the present paper which are bordered posteriorly by the occipital furrow.

Onnia superba, like *O.*? *cobboldi* and unlike *O. gracilis* and *O. ornata*, has three continuous rows of pits in front of the glabella. It is readily distinguished, however, from the former species by the usually more angular cephalon, the much larger number of pits in E_2, including several more auxiliary pits distributed fairly evenly along all parts of the fringe, and by the large number of auxiliary pits in I_{2-4}. The incomplete cephalon figured by Størmer (1930 : pl. 6, fig. 13) as *Cryptolithus* cf. *portlocki* (Salter) shows several features, such as the possession of three continuous rows of pits frontally, the extension of E_2, which is composed of numerous small pits, to the genal angle, the presence in E_1 and I_1 of larger pits than in neighbouring rows, and the apparent existence of radial sulci internal to I_1, which suggest that it is actually an *Onnia*, probably related to *O. superba*. It appears to differ from the Shropshire species, however, in having a slightly higher pit count for at least the three outermost rows, but a more detailed comparison must await the examination of additional material.

The Norwegian species is interesting and important in that it extends the known range of *Onnia* both geographically and stratigraphically as the species, being associated with *Tretaspis latilimba* Linnarsson, is apparently from Stage 4cβ, an horizon at least approximately equivalent to the lower part of the Ashgill Series. In Britain no records of *Onnia* are known after the *Dicranograptus clingani* Zone, but the genus occurs with *Tretaspis* in the Onnian of the Cross Fell Inlier.

In the present paper the trinucleid figured as *Onnia* aff. *superba* (Pl. 19, fig. 10) is of particular importance on account of the horizon from which it was collected, the *Onnia gracilis* Zone. *O.* aff. *superba* differs from *O. superba* itself in having a few more pits in E_1 and I_1, but, like that species, has only three continuous rows of pits in front of the glabella compared with four in *O. gracilis* with which it is associated. It is possible, or even likely, that *O.* aff. *superba* represents a link between *O.*? *cobboldi* and *O. superba*, but more material of this rare form is needed.

It has been pointed out earlier (see p. 128) that the trinucleid from Venezuela assigned by Whittington to *Onnia* does not belong to the genus and is probably best regarded as a *Salterolithus*. Rusconi (1956 : 9, pl. 1, fig. 11) has also described a so-called *Onnia*, *O. verrucosa*, from the Mendoza district of Argentina. His only illustration is inadequate, but shows a short cephalon with conspicuous lateral ocelli just outside the axial furrows and a fringe which clearly bears no resemblance to that of *Onnia*. A detailed comparison must await further illustration of the species, but it seems fairly certain that a genuine *Onnia* has not yet been discovered in South America.

IV. THE DEVELOPMENT AND RELATIONSHIPS OF THE TRINUCLEIDAE IN SOUTH SHROPSHIRE

Bancroft's views on some of the Caradoc Trinucleidae were summarized briefly in a short paper (1935) in which the following opinions were expressed.

(*a*) There is a line of descent from *Marrolithus*, with no E_2 row, to *Reuscholithus*, with E_2 frontally and posterolaterally, by way of late Costonian forms (presumably those now termed *Costonia*) in which E_2 is developed frontally.

(*b*) Another line of descent is *Salterolithus* → *Ulricholithus* → *Broeggerolithus* → *Cryptolithus* (*s.s.*). Apparently Bancroft believed the first true *Cryptolithus* to be *C. tesselatus* Green, which he stated to occur in the Upper Longvillian of the U.S.A.

He drew attention to the fact that *C. tesselatus* differed from *Broeggerolithus soudleyensis* only in the complete absence of E_2, and implied that the latter species was ancestral to the former.

After examining numerous trinucleids from horizons throughout most of the Caradoc Series, the author agrees with certain features of Bancroft's claimed " lines of descent ", but cannot subscribe to others. In general, Bancroft's views appear to represent an over-simplification of the position, and current views on Caradoc correlations and trilobite distribution differ in many respects from those of even a few years ago. Knowledge of trinucleid evolution and distribution is still far from complete and the following remarks summarize the present position with regard to the Caradoc faunas of Shropshire.

There appear to have been at least three lines of trinucleid evolution during the Costonian Stage (late *Nemagraptus gracilis* Zone) in Shropshire. The first of these concerns for the most part the genus *Marrolithus*, which was abundant in the Anglo-Welsh Area throughout the Upper Llanvirn and Llandeilo Series and continued with little change into the Harnagian Stage (Spy Wood Grit) of the Shelve Inlier. The history of the group is unknown in south-east Shropshire until the topmost Costonian Stage, where the genus *Costonia* retains sufficient *Marrolithus*-like characters, such as subangular cephalic outline and anterolateral inflation of the fringe, to suggest that it represents a local offshoot from the main *Marrolithus* stem. As described earlier in this paper, the derivation of *Reuscholithus* from *Costonia elegans* appears to be comparatively straightforward, but no evidence has been found for the continuation of this line of development and *Reuscholithus* itself is probably earlier in age than the last-known members of the ancestral *Marrolithus* group in the Spy Wood Grit of the Shelve Inlier.

The earliest other trinucleids found in south Shropshire are *Broeggerolithus* (*s.l.*), *Salterolithus* and *Smeathenia*, all of which appear almost simultaneously in the early Harnagian Stage. Their pre-Harnagian history is as yet unknown, but *Broeggerolithus* is found west of Bala at what may be a slightly lower horizon, though this is not certain, so that its migration from still farther west is possible. Whether or not the three genera derived from a common ancestor such as *Lloydolithus*, to which *Salterolithus* bears some resemblance, from the base of the Harnagian onwards they represent two separate lines of evolution. On the one hand is *Broeggerolithus*, and on the other are the probably interrelated *Salterolithus* and *Smeathenia*. In the present work the former *Salterolithus harnagensis* is placed in *Broeggerolithus* (*s.l.*), and this Harnagian form probably developed into typical *Broeggerolithus* (*s.s.*) of the *broeggeri* type through *Broeggerolithus ulrichi* by means of : *a*. suppression of numerous auxiliary pits, some of them irregularly arranged, *b*. accentuation of straight, sometimes slot-like, radial rows of pits, *c*. formation of raised interradial ridges, especially in E_1, *d*. loss of some pits of E_2 at the genal angles, though this trend is partially reversed in the last-known species of *Broeggerolithus*, and *e*. stronger development of the pit walls compared with the size of pit, so as to form both radial and concentric " bands ". That the above account may yet prove to be an over-simplification is suggested by the fact that Harper (1956 : 386) has recorded *Salterolithus harnagensis* from near Llanystwmdwy, Caernarvonshire in company with

Broeggerolithus in which some pits of E_2 are absent frontally, but unfortunately no figures of this material are yet available for comparison.

The evolution of *Broeggerolithus* in the Lower Longvillian is interesting as there are three types present, viz.:—

1. It may be assumed that *B. soudleyensis* existed in south Shropshire during the Lower Longvillian, though it has not yet been found, as the species occurs in the Upper Longvillian virtually unchanged from the Soudleyan form. It has been recorded from the Lower Longvillian of the Berwyn Hills (Whittington, 1938*a* : 451), and its apparent absence from Shropshire is probably due to the development there of massive sandstones in the Lower Longvillian, representing an environment in which trinucleids do not occur so abundantly as in mudstones.

2. *Broeggerolithus globiceps* has a few pits of E_2 absent anteriorly, but other differences from *B. soudleyensis* are marked and the two species can only be distantly related, though possibly originating from an ancestral *B. broeggeri*.

3. *Broeggerolithus simplex* sp. nov., with its fully developed E_2, lack of a raised E_1, and much less well-developed interradial ridges, is reminiscent of the Upper Longvillian and Marshbrookian species, of which it may be the forerunner, and is distinct from *B. globiceps*.

The ensuing development of *Broeggerolithus* through the Upper Longvillian and Marshbrookian, with *B. longiceps* and *B. transiens* respectively, is reasonably straightforward and the latter shows, as the name implies, some features, for example the increase in the size of pits in E_1 and I_1, which might appear to mark a transition to the genus *Onnia*. However, such a transition cannot yet be said to be completely established, and the stratigraphically intervening Actonian Stage has not yet yielded identifiable trinucleids. In Bohemian faunas *Onnia*, as represented by *O. ornata* (Sternberg), is long ranging and earlier than the British occurrences, but appears to be closely related only to *O. gracilis*, so that one could postulate a migration from Europe during the Onnian, giving rise to the Shropshire *Onnia gracilis* as an alternative, and perhaps in addition, to evolution from an indigenous stock. As has been noted earlier in this paper, there are difficulties in the acceptance of a simple line of evolution within the relatively short sequence of the Shropshire Onniae. *O.? cobboldi* and *O. superba* resemble each other more closely than they do the stratigraphically intermediate *O. gracilis*, and the mutual relationships are not yet fully resolved, though the figured *O.* aff. *superba* suggests a connection. After the close of the Onnian Stage in England and Wales *Onnia* has been found only in southern Norway, and the history of the group is, on the whole, poorly known. It may be noted that according to Bancroft (*in* Lamont, 1948 : 416) the *Onnia gracilis* Zone in the Cross Fell Inlier may follow a disconformity in the succession. In the Welshpool district the Gwern-y-brain Shales containing *Onnia gracilis* overlie the Gaer Fawr Beds of Longvillian age, and it is possible that an extension of marine conditions over parts of England and Wales during Onnian times led to a renewal of links with extra-British faunas in southern Europe which had not been in evidence since the early part of the Caradoc Series.

Of the early forms of *Broeggerolithus* the link between *B. broeggeri* and *B. globiceps* is not yet established, and the stratigraphically intermediate *B. soudleyensis* probably represents only an off-shoot which left the main *Broeggerolithus* line of descent during the Lower Soudleyan and continued a parallel line of development up to and including the lower part of the Upper Longvillian without undergoing any significant change of fringe-type. Whittard (1958 : 71) has now discovered *Cryptolithus* (*s.s.*) in the Upper Llanvirn Series and the Llandeilo Series of the Shelve Inlier, so that one can no longer support Bancroft's claim (1935 : 334) that *Broeggerolithus* from the Caradoc gave rise to *Cryptolithus* in the U.S.A., presumably by means of migration from Britain.

Of the other Harnagian genera mentioned earlier in this paper, *Salterolithus* continued throughout the Harnagian and the Lower Soudleyan, when apparently it became extinct without, so far as is known, giving rise to any later forms. The related *Smeathenia* is restricted, both horizontally and vertically, in its distribution, and may represent only a short-lived local development in which the formation of rows of pits external to the girder reached an unusually high level.

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PLATES

Specimens whitened with ammonium chloride. Prefixes refer to collections in the following institutions :

BM. I. or In. = British Museum (Nat. Hist.), London.
BU. = University of Bristol, Department of Geology.
GSM. = Geological Survey & Museum, London.
SM. A. = Sedgwick Museum, Cambridge.

PLATE 11

Ampyxella edgelli (Reed) . . . . . p. 80

Onnian Stage, *O. superba* Zone, north bank of River Onny, 720 yards west-south-west of Wistanstow Church.

FIG. 1. Whole individual, preserved as internal mould, showing anterior spine and thorax. SM. A. 43831. × 2.

FIG. 3. Lectotype, a slightly flattened cranidium preserved as an internal mould. GSM. 35648. × 2·2.

FIG. 4. Internal mould of glabella showing uncrushed outline and median carina. BM. In. 49724. × 2·5.

FIG. 7. Latex cast of pygidium showing marginal rim and steeply-declined border with terrace-lines. BM. In 37612. × 4.

Actonian Stage, south bank of River Onny 80 yards west of junction of river and Batch Gutter.

FIG. 6. Latex cast of whole individual. BU. 8312. × 2·5.

Lonchodomas pennatus (La Touche) . . . . p. 82

Actonian Stage, locality probably as Fig. 6.

FIGS. 2, 5. Internal mould of cranidium showing hypostomal pits and glabellar muscle-areas. B.M. In. 48561. × 2.

Onnian Stage, *O. gracilis* Zone, north bank of River Onny 85 yards east of junction of river and Batch Gutter.

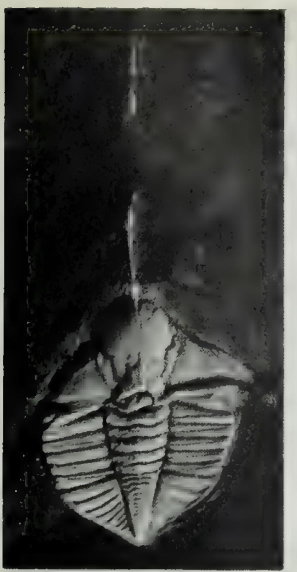
FIG. 8. Thorax, pygidium and incomplete free cheek with test preserved. BM. In. 48935. × 2·75.

FIGS. 9, 11. Testate pygidium photographed whitened and then wet to show pygidial muscle-scars. BM. In. 48934. 9, × 2·65. 11, × 2·75.

FIG. 10. Incomplete cranidium showing grooved frontal spine. BM. In. 48939. × 3·25.

Onnian Stage, *O. superba* Zone, locality as Fig. 1.

FIG. 12. Holotype, internal mould of a cranidium. BM. In. 37621. × 2·5. Photographs 1, 8, 10–12 by Mr. J. Brown, 6 by Mr. E. W. Seavill, the remainder by the writer.



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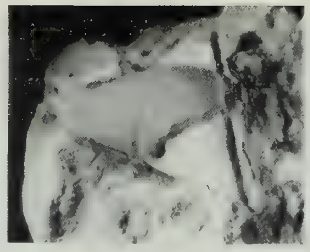

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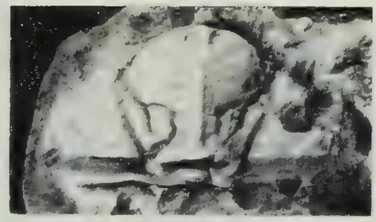

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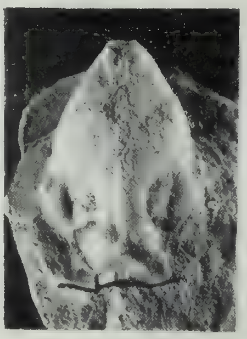

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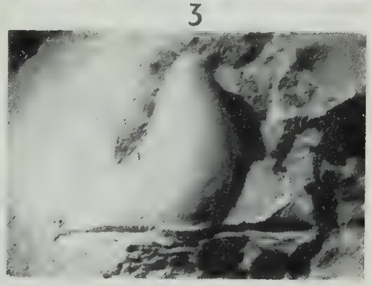

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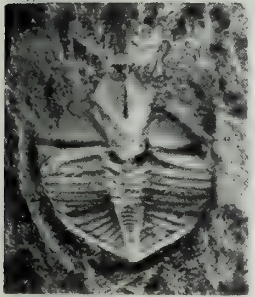

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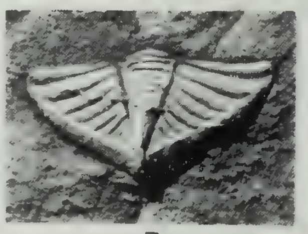

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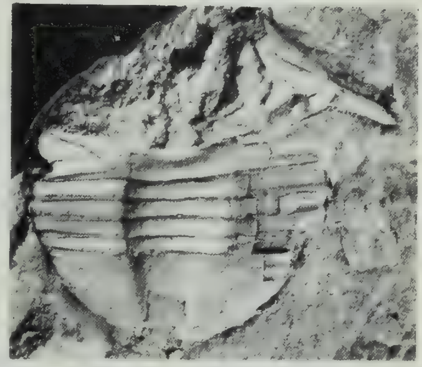

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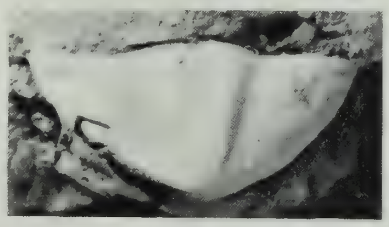

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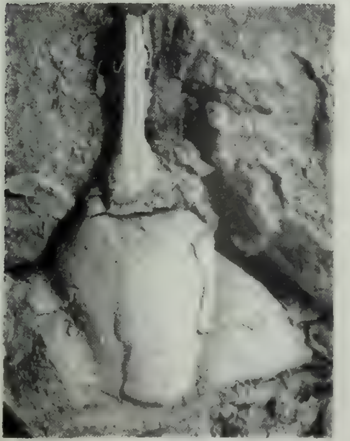

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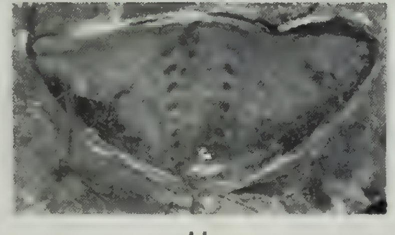

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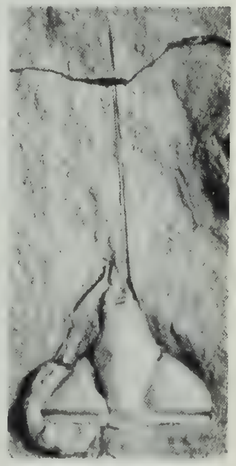

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PLATE 12

Costonia ultima (Bancroft) . . . . . p. 87

Costonian Stage, *C. ultima* Beds, old quarry 500 feet south of Coston Farm, 1 mile east of Clunbury.

FIGS. 1, 3. Internal mould of whole individual, showing thorax. B.M In. 54031. × 3.

FIGS. 2, 5. Internal mould of cephalon and impression of lower lamella with girder and pseudogirders. BM. In. 54036. × 3.

FIG. 4. Latex cast of external mould to show development of E_2 frontally. BM. In. 48942. × 2·25.

FIG. 7. Internal mould of cephalon showing pit arrangement and median ocellus. BM. In. 54033. × 3.

FIG. 8. Latex cast of external mould of thorax and pygidium. BM. In. 48940. × 2·5.

FIG. 9. Latex cast of external mould of cephalon. Note cephalic outline frontally and occipital spine. BM. In. 54032. × 3.

FIG. 10. Latex cast of holotype external mould. BM. In. 43489. × 3·25.

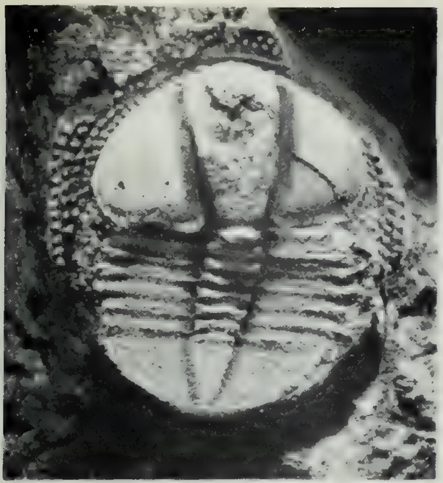
FIG. 11. Latex cast of cephalon. BM. In. 54034. × 3.

FIG. 12. Latex cast to show occipital spine and inflation of pits in I_1 anterolaterally. BM. In. 48941. × 2·25.

Old quarry in Brokenstones Plantation, 1600 yards north-east of Horderley Station. Horizon as for Fig. 1.

FIG. 6. Internal mould of pygidium. BM. In. 54035. × 2·25.

Photographs 4, 8 and 12 by Mr. J. Brown, the remainder by the writer.



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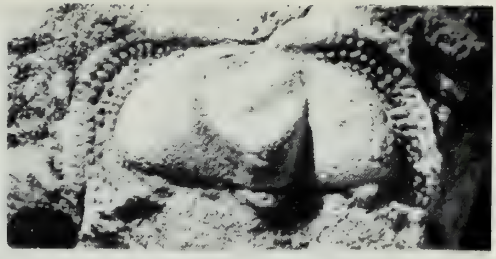

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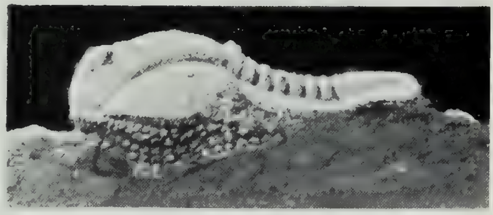

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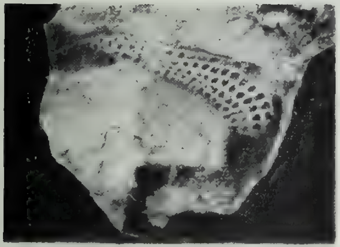

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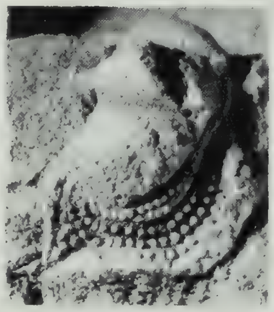

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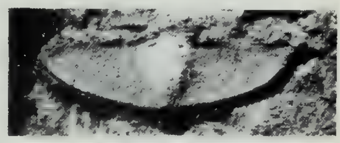

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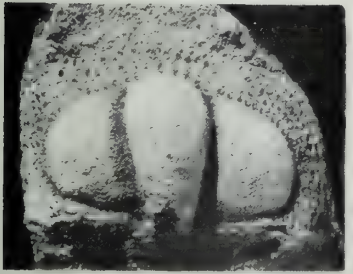

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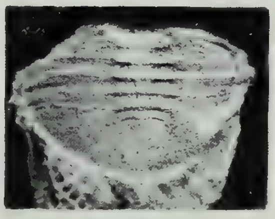

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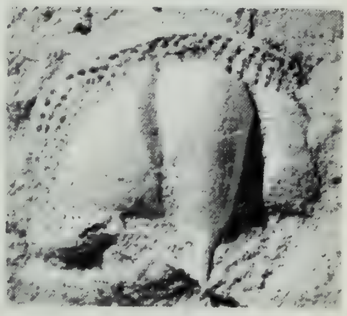

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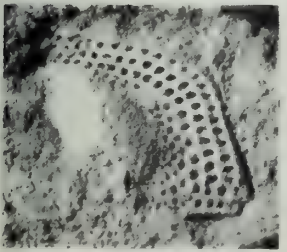

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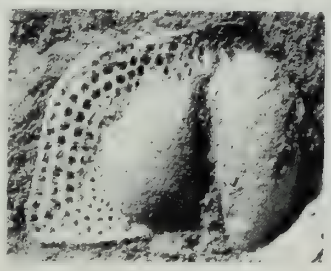

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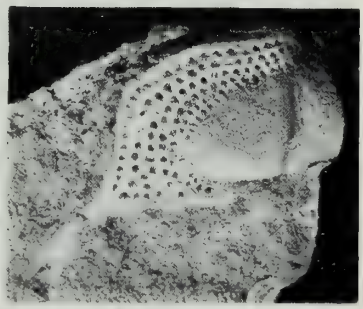

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PLATE 13

Costonia elegans sp. nov. . . . . . p. 89

Costonian Stage, *Harknessella subquadrata* Limestone, old quarry in north-eastern part of Round Nursery, 1380 feet south-south-east of Harnage Grange.

FIGS. 1, 2, 4. Holotype cephalon with test preserved. BM. In. 49744. × 2.

FIG. 3. Immature cephalon showing large number of small pits in E_1. BM. In. 49733. × 3·75.

FIG. 5. Incomplete cephalon with E_2 developed anteriorly as far as R5. BM. In. 49745. × 3.

FIG. 6. Immature cephalon lacking inflated pits at anterolateral angles. BM. In. 49747. × 3.

FIG. 9. Latex cast of fragmentary young individual showing reticulation of cheek-lobe. BM. In. 49746. × 8.

Old quarry in Black Dick's Coppice, Evenwood. Horizon as for Fig. 1.

FIG. 8. Immature pygidium. B.M. In. 49311. × 4.

Smeathenia smeathenensis (Bancroft) . . . . p. 100

Harnagian Stage, *Reuscholithus reuschi* Zone, section in old cartway near south end of Smeathen Wood, Horderley, 250 yards west-south-west of Wood House.

FIG. 7. External mould of underside of fringe showing girder and pseudogirder. BM. In. 49132. × 2·5.

FIGS. 10–12. Cephalon with a few gaps in E_4, and E_5 not yet developed. Note also median ocellus. BM. In. 49560. × 2·5.

FIG. 13. Small individual with reticulate cheek-lobes and only three rows of pits external to the girder. BM. In. 50619. × 4.

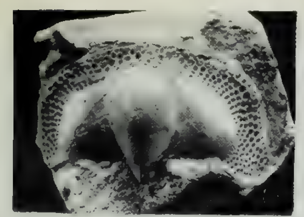
FIG. 15. External mould of pygidium. BM. In. 42092. × 2·7.

FIG. 16. Lectotype, internal mould of mature cephalon. BM. In. 43321. × 2·3.

Exposure in field 550 yards north-west of Woolston House, Woolston. Horizon as for Fig. 7.

FIG. 14. Latex cast of immature cephalon with reticulate cheek-lobes yet possessing well-developed E_4. BM. In. 50767. × 4.

Photographs 1, 2 and 4 by Mr. E. W. Seavill, 6–8 by Mr. J. Brown, the remainder by the writer.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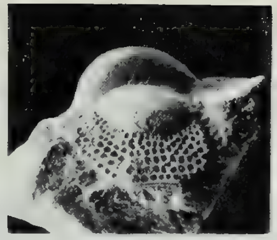
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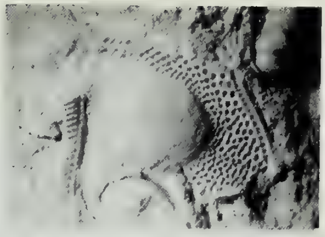
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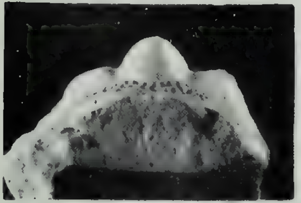
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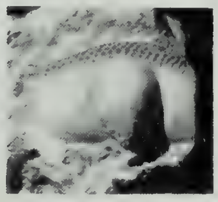
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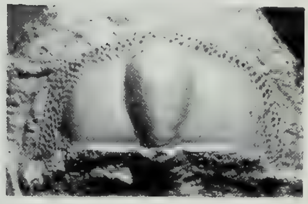
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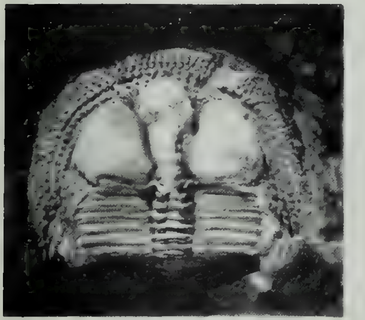
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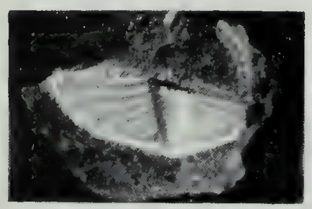
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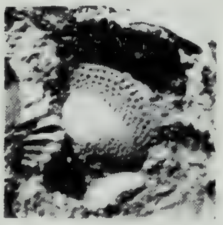
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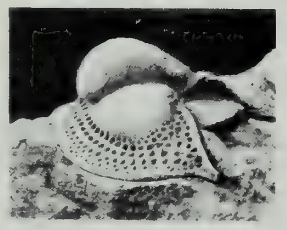
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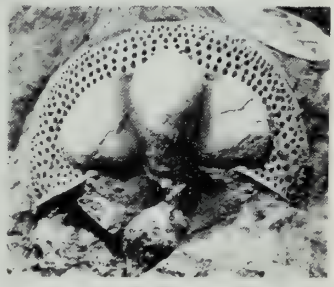
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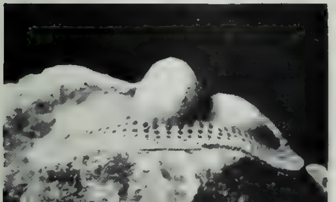
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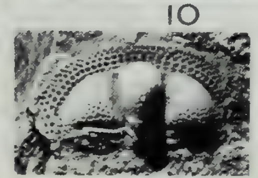
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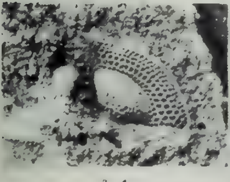
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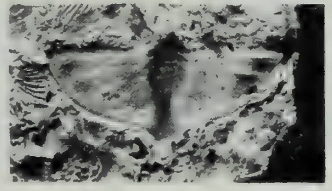
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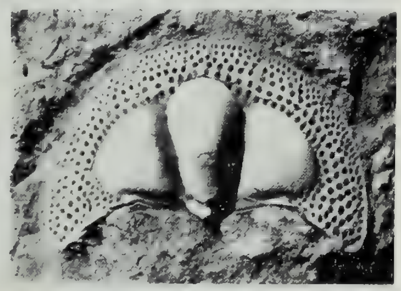
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PLATE 14

Reuscholithus reuschi Bancroft . . . . p. 91

Harnagian Stage, *R. reuschi* Zone, section in old cartway near south end of Smeathen Wood, Horderley, 250 yards west-south-west of Wood House.

FIGS. 1, 3. Latex cast and internal mould of holotype. BM. In. 42080 *a* & *b*. × 2·75.

FIG. 7. Internal mould of immature cephalon showing relatively large breadth and median ocellus. BM. In. 50517. × 3·25.

South bank of stream 525 yards east of Gutter Farm, 1½ miles east-north-east of Hope Bowdler. Horizon as for Fig. 1.

FIG. 2. Young individual (? Meraspis Degree 5) with four complete rows of pits and short ocular ridges. BM. In. 50688. × 4·5.

FIG. 9. Underside of fringe showing girder, genal spines, and the irregular development of E_2. BM. In. 49316. × 2.

FIG. 12. Immature cephalon (? Holaspis) with reticulate surface and median ocellus, but lacking alar lobes. BM. In. 49317. × 4.

By north bank of Coundmoor Brook, 1300 yards south-west of Harnage Farm. Horizon as for Fig. 1.

FIG. 4. Probably young Holaspis with fine reticulation on parts of cheek-lobes and thoracic segments. BM. In. 51501. × 3.

FIG. 5. Immature cephalon, appearing longer due to distortion, with reticulate surface and alar lobes. BM. In. 50671. × 5·5.

FIG. 6. Wide immature cephalon with strong ocular ridges and ocelli. BM. In. 54028. × 7.

FIG. 10. Two young individuals (Meraspis Degree 5), preserved as internal and external moulds, showing reticulation, strong alar lobes, and long genal spines. BM. In. 50665. × 4·5.

FIG. 11. Smallest known cephalon, showing ocular ridges and the forward position of the genal angles. BM. In. 50667. × 8.

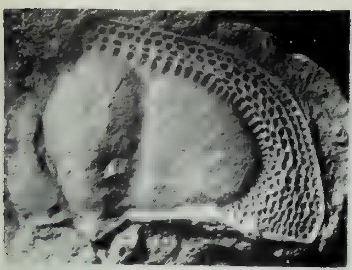
FIG. 13. Internal mould of right half of fringe showing random arrangement of pits, particularly towards the genal angle. BM. In. 50668. × 4.

FIG. 14. Internal mould of almost complete individual, to show semi-elliptical form of mature pygidium. BM. In. 50672. × 3·5.

North bank of Coundmoor Brook, 1310 yards south-west of Harnage Farm. Horizon as for Fig. 1.

FIG. 8. Internal mould of large cephalon. BM. In 50519. × 2·7.

Photographs by the writer.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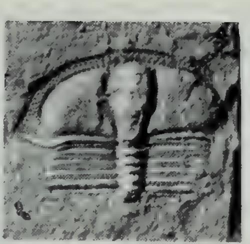
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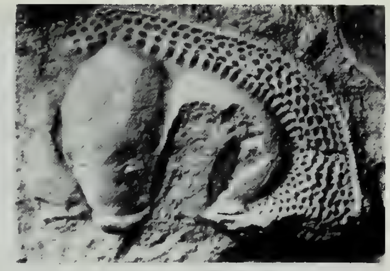
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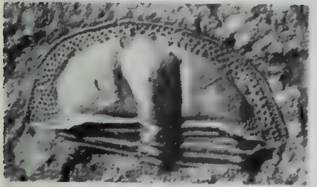
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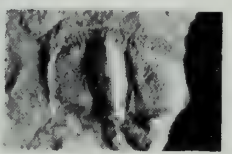
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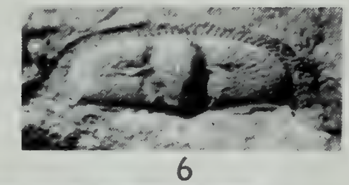
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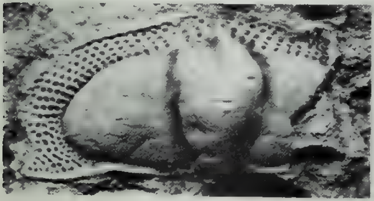
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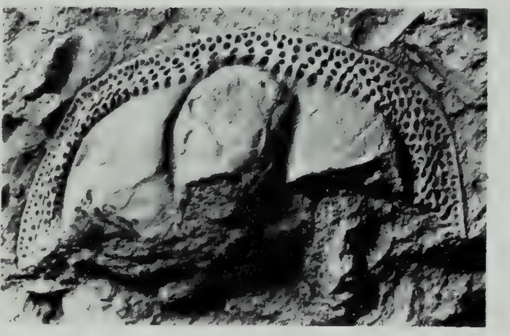
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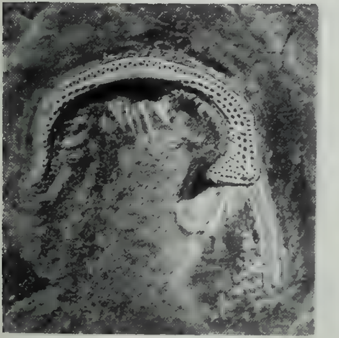
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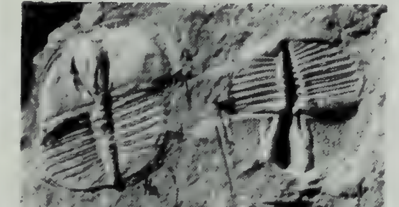
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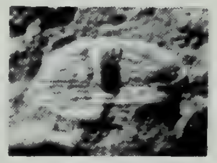
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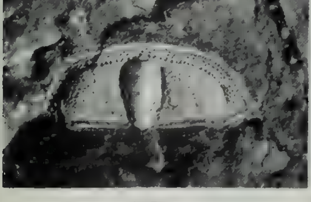
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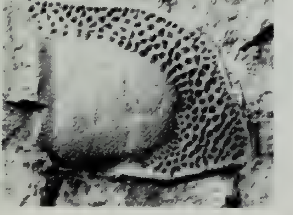
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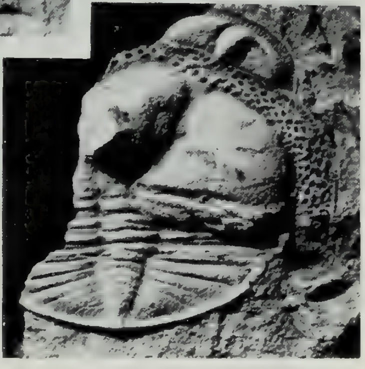
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PLATE 15

Salterolithus caractaci (Murchison) . . . . p. 96

Harnagian Stage, *S. caractaci* Zone, excavation 700 feet north of Glenburrell Farm, Horderley.

FIG. 1. Latex cast of whole individual. BM. In. 51339. × 2·1.

FIG. 2. Latex cast of cephalon. BM. In. 51340. × 2·4.

Soudleyan Stage, *Broeggerolithus broeggeri* Zone, stream-section at north-eastern corner of Smeathen Wood, near Horderley.

FIG. 4. External mould of underside of fringe. BM. In. 51207. × 2·3.

FIG. 9. Internal mould of cephalon. BM. In. 51205. × 2.

Section behind north-west end of Glenburrell Farm, Horderley. Horizon as for Fig. 4.

FIG. 6. Internal mould of fringe showing underside. BM. In. 51193. × 2·8.

Salterolithus praecursor sp. nov. . . . p. 89

Harnagian Stage, *Reuscholithus reuschi* Zone, south bank of Coundmoor Brook, 1356 yards south-west of Harnage Farm.

FIG. 8. Internal mould of immature cephalon. BM. In. 52041. × 5·5.

South bank of Coundmoor Brook, 1360 yards south-west of Harnage Farm. Horizon as for Fig. 8.

FIG. 7. Immature cephalon with E_3 only slightly developed. BM. In. 51840. × 3·5.

South bank of Coundmoor Brook 1340 yards south-west of Harnage Farm. Horizon as for Fig. 8.

FIG. 3. Holotype, internal mould of cephalon. BM. In. 51479. × 3.

FIG. 5. Latex cast of incomplete cephalon showing development of E_3. BM. In. 52031. × 2·5.

FIG. 11. External mould of underside of fringe. BM. In. 52036. × 2.

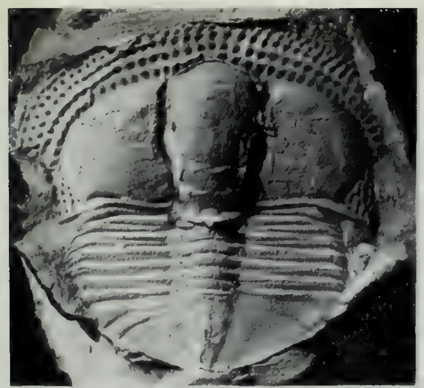
Exposure in bed of Coundmoor Brook near north bank, 1320 yards south-west of Harnage Farm. Horizon as for Fig. 8.

FIG. 10. Latex cast of cephalon with slight narrowing of fringe in front of the glabella. BM. In. 50517. × 2·7.

South bank of stream 450 yards east-south-east of Gutter Cottage, near Wallsbank. Horizon as for Fig. 8.

FIG. 12. Internal mould of young individual showing thorax and pygidium. BM. In. 54027. × 3·4.

Photograph 9 by Mr. E. W. Seavill, the remainder by the writer.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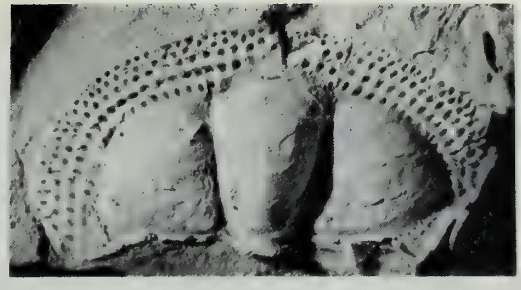
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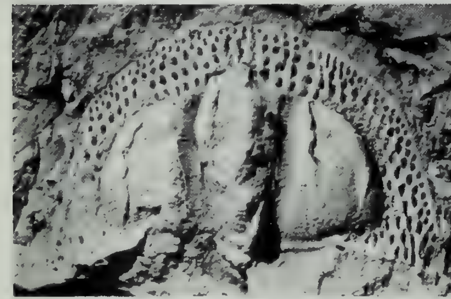
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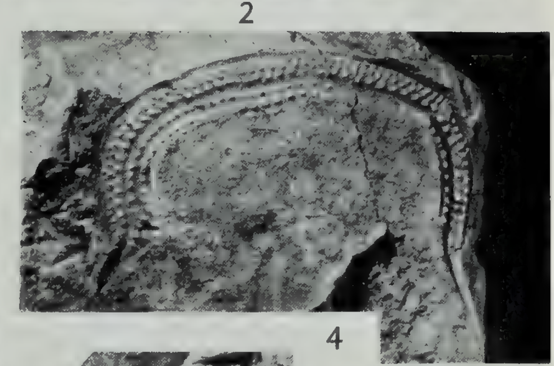
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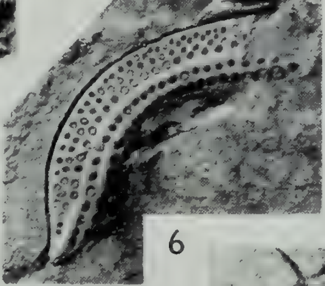
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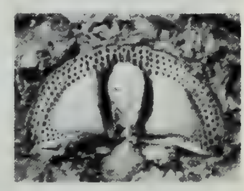
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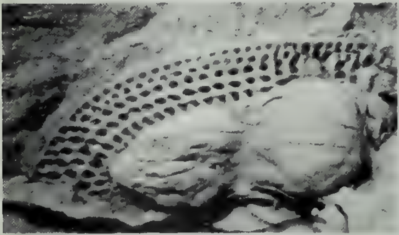
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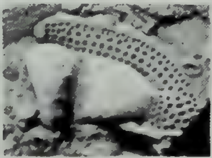
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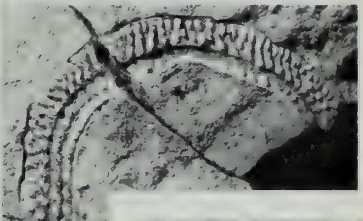
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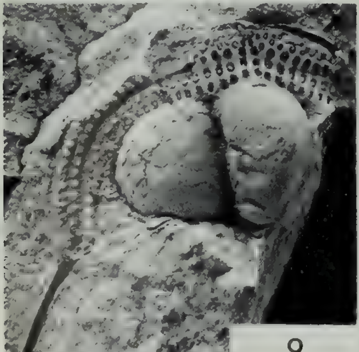
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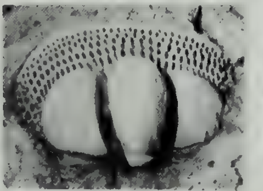
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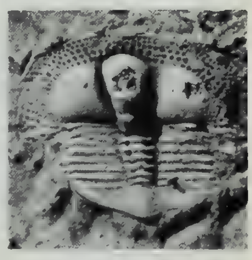
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PLATE 16

Broeggerolithus harnagensis (Bancroft) . . . p. 105

Harnagian Stage, *Reuscholithus reuschi* Zone, south bank of Coundmoor Brook, 1340 yards south-west of Harnage Farm.

FIG. 5. Lectotype, internal mould of cephalon. BM. In. 42081. × 2·6.

FIG. 13. Paratype pygidium, internal mould. BM. In. 49024. × 2·5.

South Bank of Coundmoor Brook, 1356 yards south-west of Harnage Farm. Horizon as for Fig. 5.

FIG. 9. Underside of fringe showing girder. BM. In. 54029. × 2·5.

B. harnagensis (Bancroft)? . . . . p. 106

South bank of Coundmoor Brook, 1335 yards south-west of Harnage Farm. Horizon as for Fig. 5.

FIG. 1. Internal mould of cephalon with part of test preserved. BM. In. 52041. × 3·5.

Broeggerolithus? sp. . . . . . . p. 108

Locality and horizon as for Fig. 9.

FIG. 2. Internal mould of cephalon showing irregular pits between E_1 and E_2. BM. In. 54030. × 3·3.

Broeggerolithus cf. *harnagensis* (Bancroft) . . . p. 107

Neptunian dyke in north-eastern corner of quarry in Uriconian rocks, south side of Hazler Hill, east of Church Stretton. Horizon as for Fig. 1.

FIG. 7. Incomplete cephalon showing girder and genal spine. BM. In. 50500. × 3.

FIG. 11. Fragmentary cephalon with auxiliary pits in E_2. BM. In. 42093. × 3.

Broeggerolithus broeggeri (Bancroft) . . . . p. 111

Soudleyan Stage, *B. broeggeri* Zone, stream-section at north-eastern corner of Smeathen Wood, near Horderley.

FIG. 3. Lectotype, internal mould of cephalon. BM. In. 42077. × 2·25.

FIG. 10. Internal mould of underside of fringe, showing girder and genal spine. BM. In. 50831. × 2·8.

Broeggerolithus cf. *broeggeri* (Bancroft) . . . p. 112

Locality and horizon as for Fig. 3.

FIGS. 4, 8. Internal mould of whole individual. BM. In. 48937. × 2·25.

Soudleyan Stage, *Glyptocrinus* Flags, exposure by south side of road 170 feet north-north-east of Chatwall Farm.

FIG. 14. Internal mould of cephalon. BM. In. 51447. × 2·6.

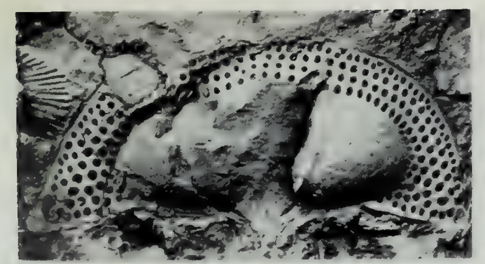
Broeggerolithus constrictus Bancroft . . . . p. 113

Stream-section 515 yards west-south-west of Ceunant, 4 miles north-north-east of Welshpool, Montgomeryshire. Horizon as for Fig. 3.

FIG. 6. Holotype. BM. In. 42101. × 3·5.

FIG. 12. Internal mould of fragmentary cephalon showing reticulate surface of cheek-lobe. BM. In. 51883. × 3·3.

Photographs 4 and 8 by Mr. E. W. Seavill, the remainder by the writer.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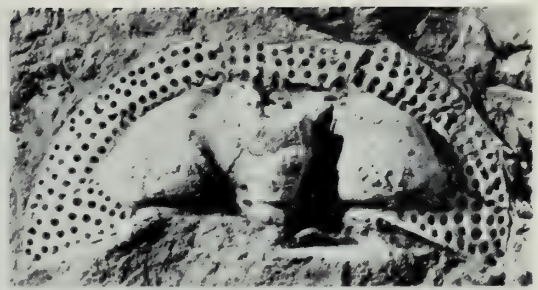
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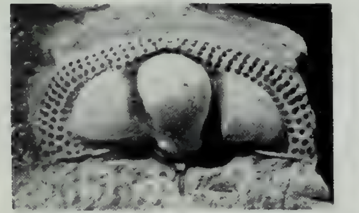
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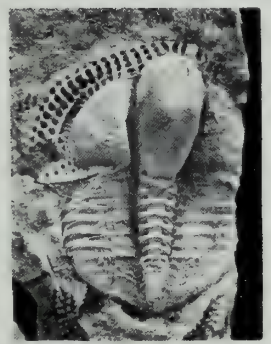
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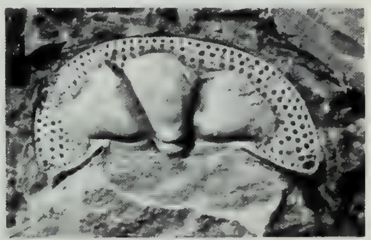
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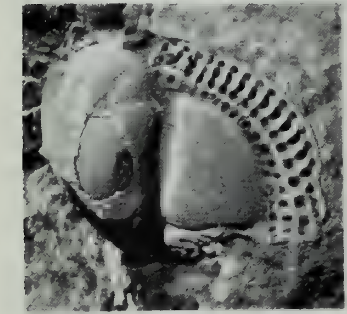
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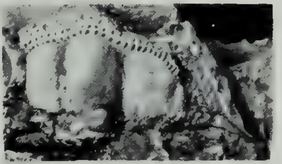
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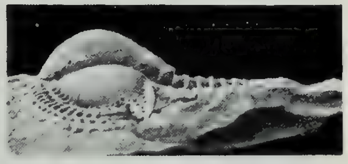
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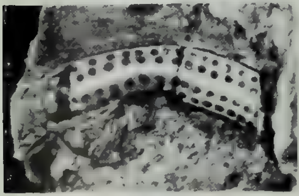
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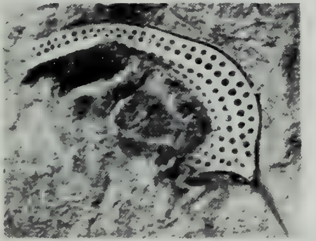
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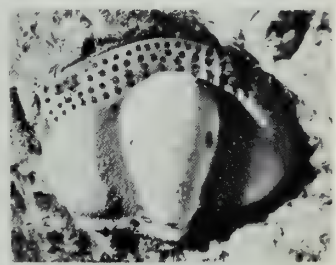
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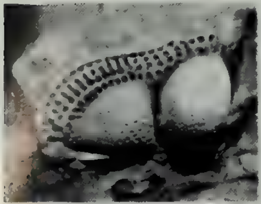
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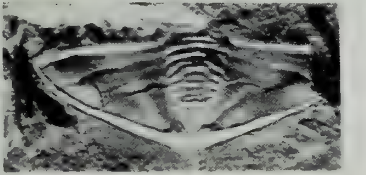
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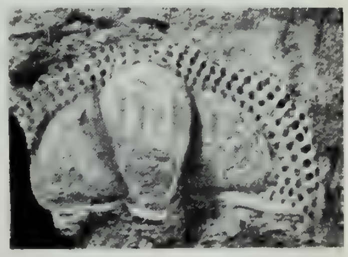
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PLATE 17

Broeggerolithus ulrichi (Bancroft) . . . . . p. 109

Harnagian Stage, *B. ulrichi* Zone, stream-section 120 yards west-north-west of Middle House $3\frac{1}{2}$ miles north of Welshpool, Montgomeryshire.

FIG. 10. Internal mould of pygidium. BM. In. 49708. × 2·7.

FIG. 11. Internal mould of cephalon showing auxiliary pits in E_2 in frontal part of fringe. BM. In. 54024. × 1·5.

Broeggerolithus soudleyensis (Bancroft) . . . . p. 115

Lower Soudleyan, *Broeggerolithus broeggeri* Zone, stream-section at north-eastern corner of Smeathen Wood, near Horderley.

FIG. 5. Underside of fringe showing girder and 3 pits of E_2 absent frontally. BM. In. 51446. × 2·6.

FIG. 6. Underside of fringe with 2 pits of E_2 absent frontally. Note also girder and genal spine. BM. In. 51445. × 2·6.

Upper Soudleyan, *B. soudleyensis* Zone, Soudley Quarry, just south-east of Soudley Pool.

FIG. 1. Internal mould of fringe. Note absence frontally of 3 pits of E_2, and corresponding slight flattening of cephalic outline. BM. In. 49314. × 2·5.

FIGS. 9, 17. Internal mould of cephalon with 7 pits of E_2 absent frontally. BM. In. 54025. × 2·5.

Old quarry by north-east side of road 100 yards south-east of Glenburrell farm, Horderley. Horizon as for Fig. 1.

FIG. 7. Internal mould of small cephalon with 7 pits of E_2 absent frontally. BM. In. 50586. × 2·8.

FIG. 8. Underside of fringe showing girder, and pits of E_2 absent frontally from R 0–2 and R 5–6. BM. In. 52856. × 2·5.

Upper Longvillian Substage, *Kjaerina bipartita* Zone, locality as for Fig. 1.

FIGS. 2–4. Cephalon with test preserved and 6 pits of E_2 absent frontally. BM. In. 50584. Figs. 2, 3, × 3. Fig. 4, × 4.

Broeggerolithus globiceps (Bancroft) . . . . p. 117

Lower Longvillian Substage, Zone of *Dalmanella indica* and *D. lepta*, just east of south-western corner of Rookery Wood, south-east of Horderley.

FIG. 13. Internal mould of cephalon showing large glabella and 3 pits of E_2 absent frontally. BM. In. 49315. × 2.

FIG. 15. Lectotype, internal mould of cephalon with 3 pits of $E_2 + e_2$ absent frontally and 4 absent at the genal angle. BM. In. 42076. × 2·25.

FIG. 16. Internal mould of cephalon. Note interradial ridges and only 2 pits of E_2 absent at genal angle. BM. In. 49321. × 2·5.

Broeggerolithus sp. (? nov.) . . . . . p. 119

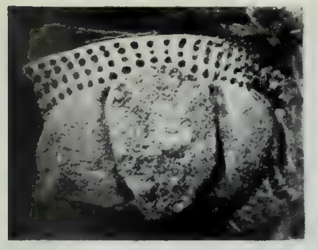
Locality and horizon as for Fig. 13.

FIG. 12. Internal mould of cephalon. BM. In. 49313. × 2·25.

Broeggerolithus simplex sp. nov. . . . . p. 120

FIG. 14. Holotype, internal mould of cephalon. BM. In. 50614. × 3.

Photographs 1, 12, 13, 15 and 16 by Mr. J. Brown, 2–4 and 14 by Mr. E. W. Seavill, the remainder by the writer.



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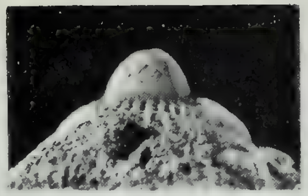

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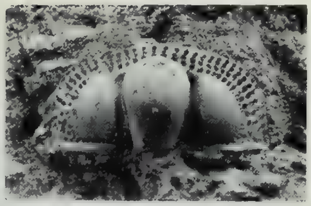

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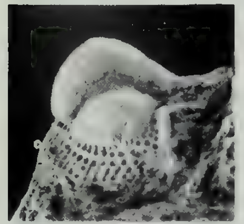

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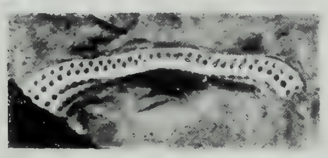

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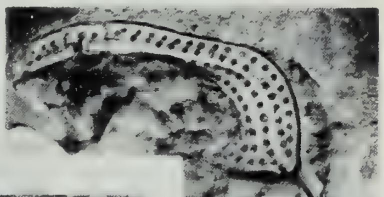

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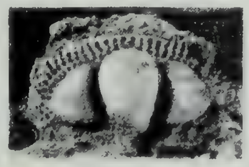

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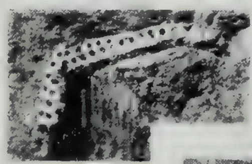

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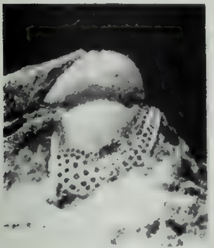

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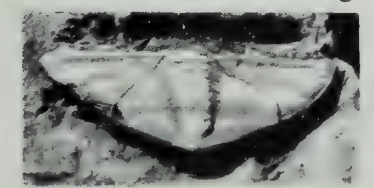

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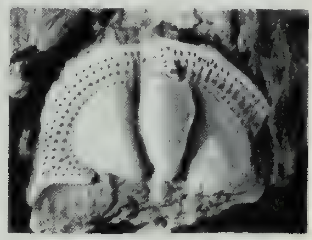

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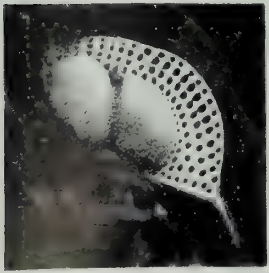

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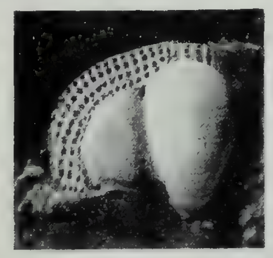

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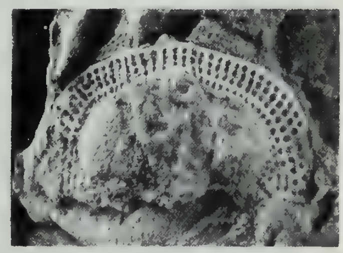

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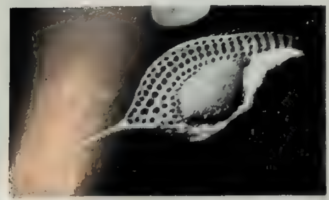

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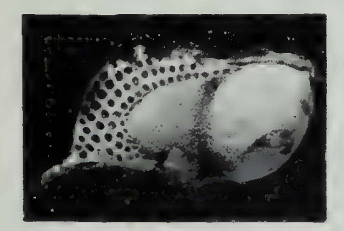

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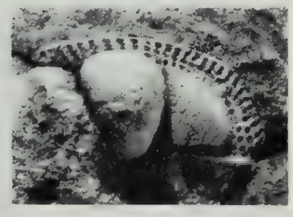

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PLATE 18

Broeggerolithus longiceps (Bancroft) . . . . p. 121

Upper Longvillian Substage, *Kjaerina bipartita* Zone, stream by west side of road 560 yards north-east of Crosspipes, nearly 2 miles north-east of Horderley Station.

FIGS. 1, 10. Internal and external mould of cephalon showing girder and genal spines. BM. In. 50661. × 1·8.

FIG. 6. Lectotype, internal mould of cephalon. BM. In. 42073. × 1·75.

Soudley Quarry, just south-east of Soudley Pool. Horizon as for Fig. 1.

FIG. 4. Internal mould of cephalon. BM. In. 50739. × 2·25.

North side of Longville Lane, 445 yards north-west of Earthwork at Cheney Longville. Horizon as for Fig. 1.

FIG. 5. Fragmentary cephalon with test preserved, showing reticulate surface of cheek-lobe. BM. In. 50591. × 3.

Broeggerolithus transiens (Bancroft) . . . p. 123

Marshbrookian Stage, *Dalmanella unguis* Zone, stream-section 550 yards south-south-west of Common Farm, near Wallsbank.

FIGS. 2, 11. Internal mould of cephalon. BM. In. 54001. × 2·75.

Marshwood Quarry, ½ mile south of Marshbrook Station. Horizon as for Fig. 2.

FIG. 3. Underside of fringe showing girder and anterior development of radial sulci in E_{1-2}. BM. In. 52050. × 2·3.

FIG. 7. Cephalon showing large glabella, swollen anteriorly. BM. In. 50594. × 2·5.

FIGS. 12, 13. Internal mould of whole individual. BM. In. 49129. × 2·7.

Marshbrookian Stage, *Onniella reuschi* Zone, by south bank of River Onny 1050 yards west-south-west of Wistanstow Church.

FIG. 8. Cephalon showing girder and impression of radial sulci in E_{1-2} on lower lamella of fringe. BM. In. 50604. × 4.

West side of road 20 yards west-north-west of Maplewall Cottage, near Woolston. Horizon as for Fig. 8.

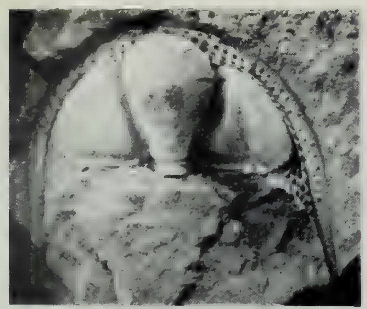
FIG. 14. Fragment of fringe illustrating flexing of radial rows of pits near the genal angle. BM. In. 50602. × 3.

Broeggerolithus cf. *transiens* (Bancroft) . . . p. 126

Well-sinking at " first house along road south from The Corner ", near Wistanstow. Horizon as for Fig. 8.

FIG. 9. Incomplete cephalon with test preserved. BM. In. 52823. × 2.

Photographs 4 and 7 by Mr. E. W. Seavill, 6 by Mr. J. Brown, the remainder by the writer.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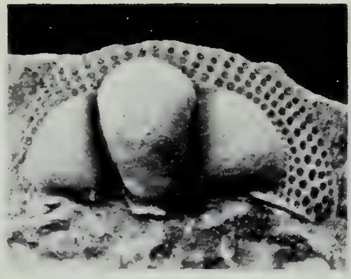
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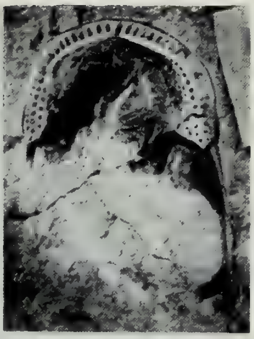
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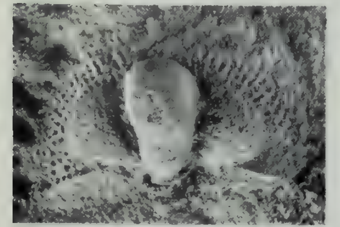
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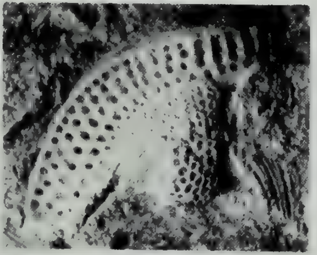
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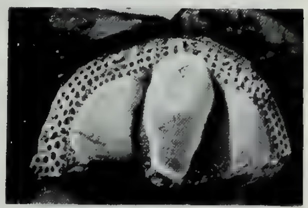
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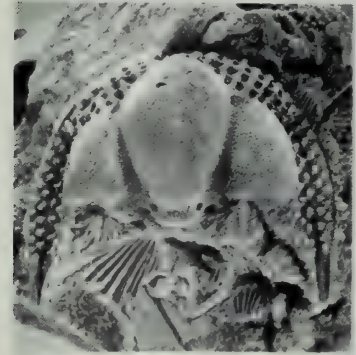
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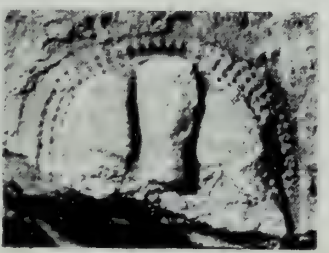
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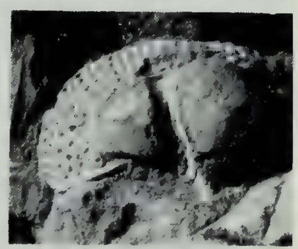
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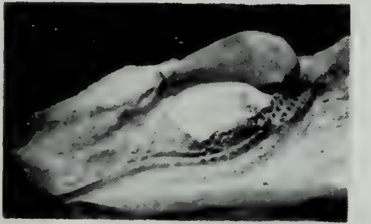
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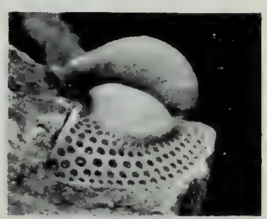
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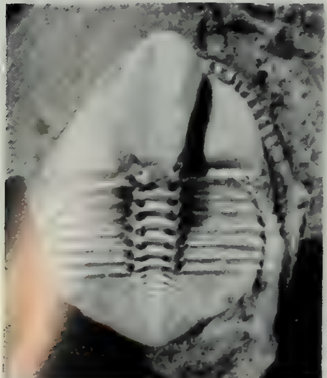
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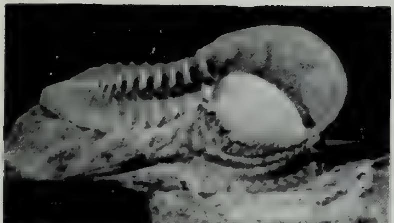
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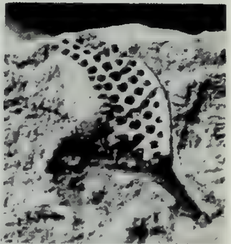
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PLATE 19

Onnia? *cobboldi* (Bancroft) . . . . . p. 128

Onnian Stage, bed of River Onny near south bank, 45 yards east of junction of river and Batch Gutter.

FIG. 1. Whole individual with test preserved. BM. In. 49028. × 2.

FIGS. 3, 12. Cephalon showing median ocellus. BM. In. 49026. Fig. 3, × 1. Fig. 12, × 2.

Onnia gracilis (Bancroft) . . . . . p. 130

Onnian Stage, north bank of River Onny 100 yards east of junction of river with Batch Gutter.

FIG. 2. Lectotype. BM. In. 42074. × 2.

FIG. 7. Paratype. Whole individual with test preserved. BM. In. 49032. × 2·1.

Onnia superba (Bancroft) . . . . . p. 133

Onnian Stage, north bank of River Onny 720 yards west-south-west of Wistanstow Church.

FIGS. 4, 5. Immature cephalon with three rows of pits in front of the glabella, and reticulate surface. BM. In. 49158. × 3·7.

FIG. 6. Immature cephalon with only two rows of pits in front of the glabella. BM. In. 49157. × 5.

FIG. 8. Latex cast of immature cephalon showing marginal suture and grooved genal spine. BM. In. 50709. × 4.

FIG. 9. Internal mould of cephalon. BM. In. 49031. × 1·5.

FIG. 11. Underside of fringe, showing strong anterior development of girder. BM. In. 49030. × 2.

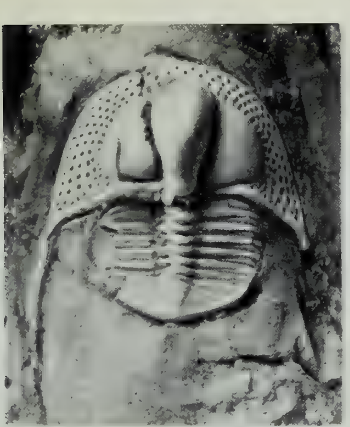
FIGS. 13, 14. Internal mould of whole individual showing pygidium and genal spines. BM. In. 49029. × 1·7.

Onnia aff. *superba* (Bancroft) . . . . . p. 136

Horizon and locality as for Fig. 2.

FIG. 10. Cephalon with test preserved. BM. In. 54037. × 1·7.

Photographs 1 and 7 by Mr. P. Green, 3–6 and 9 by Mr. J. Brown, 8 by Mr. E. W. Seavill, the remainder by the writer.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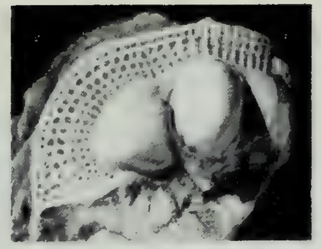
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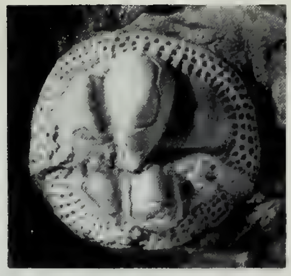
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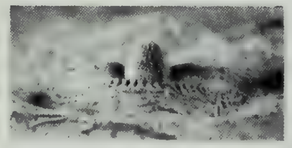
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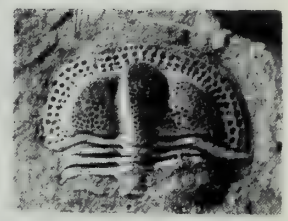
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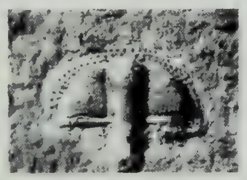
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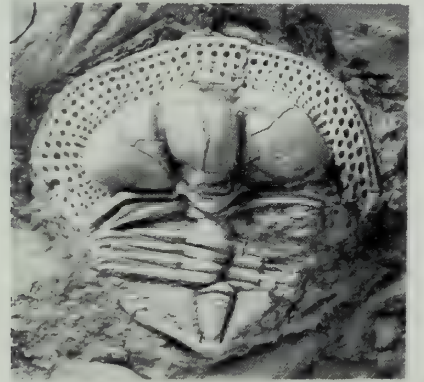
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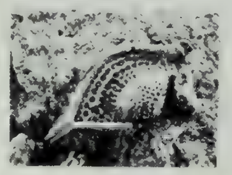
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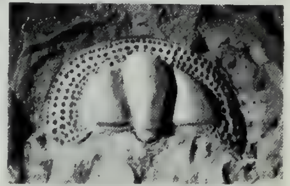
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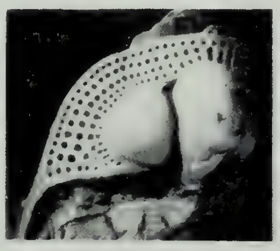
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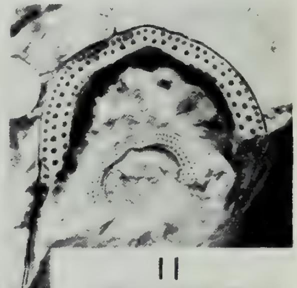
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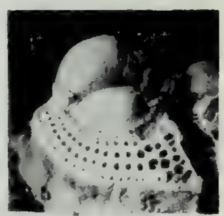
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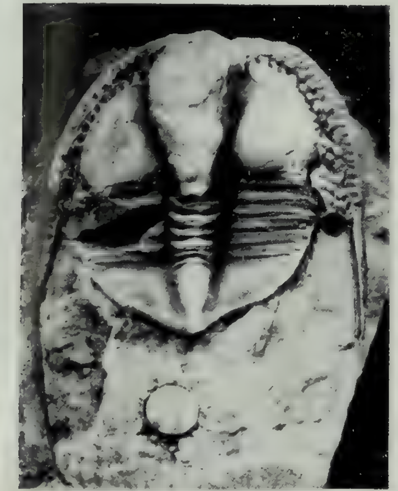
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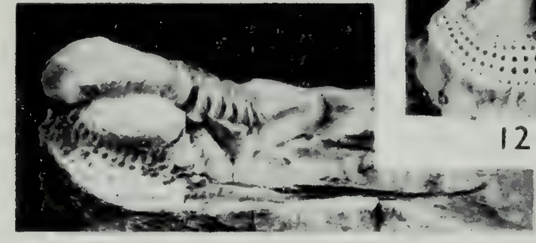
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A REVIEW OF UPPER JURASSIC PLIOSAURS

BRITISH MUSEUM
22 JUN 1960
NATURAL HISTORY

L. B. TARLO

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
GEOLOGY Vol. 4 No. 5
LONDON: 1960

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BY

LAMBERT BEVERLY TARLO

BRITISH MUSEUM
22 JUN 1960
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Pp. 145–189 ; *Plates* 20–28 ; 9 *Text-figures*

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A REVIEW OF THE UPPER JURASSIC PLIOSAURS

By L. B. TARLO

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SYNOPSIS

A systematic review is made of the thirty-six known Upper Jurassic Pliosaur species and of these only nine, representing five genera, are shown to be valid. These valid species are described and detailed comparisons made between them based on the characters of the teeth, cervical vertebrae, mandibles and scapulae. The remaining species are briefly discussed and listed in alphabetical order of their trivial names. Finally, a fully illustrated key is given for the identification of Pliosaurs.

I. INTRODUCTION

IN Mesozoic times several groups of reptiles left the land to take up life again in the sea. Of these marine reptiles the plesiosaurs are perhaps the best known. The first specimens were discovered at the beginning of the last century by Miss Mary Anning who made her living collecting and selling fossils; and the Rev. Dean Conybeare, who gave the earliest description of the plesiosaurs, made the important observation that there were forms with long necks and others with a much shorter neck (see Text-fig. 1). This review is concerned solely with the latter group which were given the name of pliosaurs after the genus *Pliosaurus* had been created by Owen in 1841.

Most of the short-necked plesiosaurians (or pliosaurs) of which the Upper Jurassic species form the central group, were described during the nineteenth century from England, France, Germany and Russia. Unfortunately there is much confusion in the literature. Some species were erected on isolated humeri and femora, some on teeth alone and yet others only on vertebrae ; and Seeley (1869) seemed to differentiate some of his species on size. Confusion was added to by authors ignoring the work of fellow palaeontologists—for example, P. Fischer and E. Deslongchamps both gave detailed descriptions and figures of identical specimens under different names. Even more unfortunate, however, was the obvious feud between Seeley and Lydekker, who steadfastly refused to recognize the generic and specific names proposed by one another. *Rhomaleosaurus* Seeley was, according to Lydekker, a synonym of *Thaumatosaurus*, whilst *Peloneustes* Lydekker was always claimed by Seeley to be

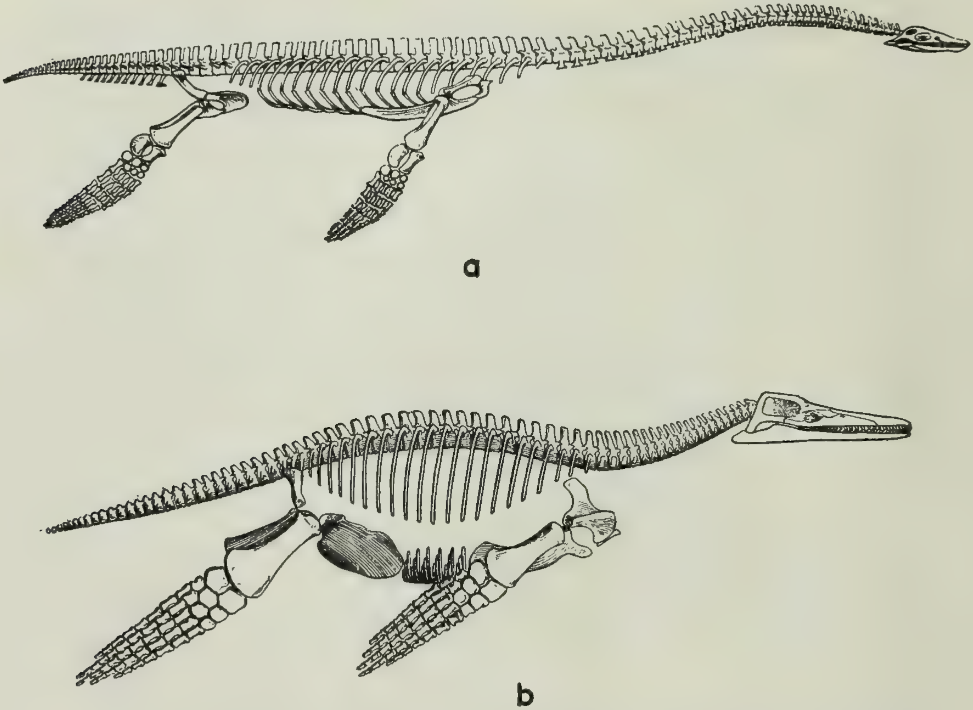

FIG. 1. *a*. Reconstruction of the Liassic *Plesiosaurus dolichodeirus* Conybeare, after Conybeare (1824). *b*. Reconstruction of the Oxfordian *Peloneustes philarchus* (Seeley), after Andrews (1913).

Pliosaurus; in addition, Seeley's specific names were generally stated by Lydekker to be synonyms of names erected years later, such as *P. sterrodeirus* Seeley (1869) taken as a synonym of *P. aequalis* Phillips, 1871. Worse still were the discrepancies in the straightforward descriptions of actual specimens. One notable mandible stated by Owen (1869) to have 24 teeth in each ramus, was later recorded by Lydekker (1889*b*) as having 30. There are in fact 25 in one ramus and 26 in the other.

Although an abundance of isolated pliosaur fragments has been described, I have concentrated attention on associated specimens, and in this way have been better able to compare the different species. The parts of the skeleton which I have found useful in making comparisons among the different species are: teeth, mandibles, cervical vertebrae, scapulae and epipodials (radii, ulnae, tibiae and fibulae). Some parts, such as the propodials (humeri and femora) are of very limited value and appear to be indistinguishable from one species to another. The teeth appear to be more useful, serving primarily to separate the Kimeridgian pliosaurs, in which the teeth are trihedral in cross-section, from those of Oxfordian age, in which they are circular. All pliosaur teeth are characterized by longitudinal ridges on the enamel of the crown, and in the Kimeridgian all the teeth of the three known species have the same ornamentation. In the Oxfordian, however, the patterns of these ridges vary and can be used to separate the six species from one another.

On the whole specific distinctions can best be effected on the characters of the cervical vertebrae, in particular the presence or absence of a ventral keel. Even this, however, must be used with caution as in all forms where a ventral keel is present it disappears towards the back of the neck where the rib articulation begins to rise from the centrum on to the neural arch.

The differences in the mandibles and scapulae are of more fundamental biological significance, and can be used as the basis for generic distinctions. Mandibles fall into two main groups both of which persist through Oxfordian and Kimeridgian times. One group, typified by *Liopleurodon ferox*, has a short symphysis which bears 5–7 pairs of large caniniform teeth, whilst the other, typified by *Pliosaurus brachydeirus*, has a longer symphysis with about 6 pairs of large caniniform teeth but with the addition of a further 5–6 pairs of smaller teeth. In Oxfordian times there were two extreme forms—*Simolestes* with a short spatulate symphysis, and *Peloneustes* with a greatly elongated symphysis.

All Oxfordian scapulae are triradiate with the dorsal process produced laterally and set off at an angle to the plane of the bone, from a ridge running from the glenoid ramus to the anterior point of the ventral plate. During the Kimeridgian striking changes took place in this bone. *Stretosaurus* has a scapula all in one plane in which the dorsal process is produced anteriorly, thus increasing the pre-glenoid length of the whole pectoral girdle. It has recently been established (Tarlo, 1959*a*) that the type of scapula common to all Oxfordian species is restricted in Kimeridgian times to pliosaurs with a long mandibular symphysis, while the *Stretosaurus* type of scapula belongs to those with a short symphysis.

This study has shown that the different skeletal elements fall into two groups—those which change with geological age and affect the whole group, such as teeth and epipodials, and those which persist through time and indicate possible phylogenetic relationships, as exemplified by mandibles. As already mentioned, the teeth and epipodials can generally be used to distinguish Oxfordian from Kimeridgian pliosaurs, while the different forms of mandible found in both ages indicate two separate lineages which can be recognized in Kimeridgian times on their radically different scapulae.

A brief description of the nine Upper Jurassic pliosaur species, which are all I now consider valid out of an original thirty-six species, is given below, and their possible phylogenetic relationship to one another is shown in Text-fig. 2. The remaining species are considered in further sections, and at the end of this paper I have given a key to the valid species which it is hoped will facilitate the identification of isolated skeletal elements.

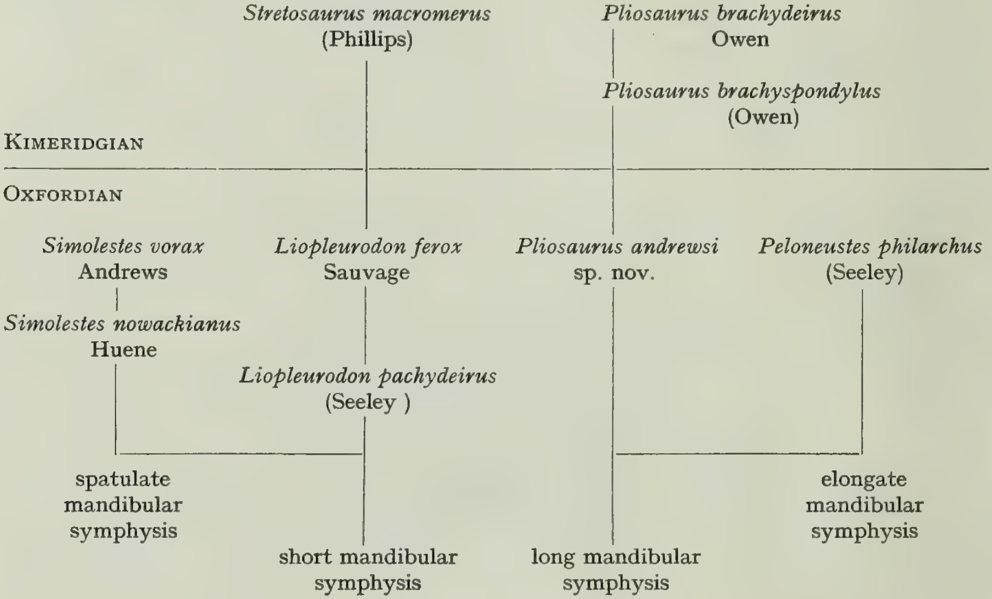
Stretosaurus macromerus (Phillips)
Pliosaurus brachydeirus Owen
Pliosaurus brachyspondylus (Owen)
Kimeridgian
Oxfordian
Simolestes vorax Andrews
Liopleurodon ferox Sauvage
Pliosaurus andrewsi sp. nov.
Peloneustes philarchus (Seeley)
Simolestes nowackianus Huene
Liopleurodon pachydeirus (Seeley)
spatulate mandibular symphysis
elongate mandibular symphysis
short mandibular symphysis
long mandibular symphysis

Fig. 2. Phylogeny of Upper Jurassic Pliosaur species.

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Photography by Messrs. A. Barlow, W. Brackenbury, J. F. Green and A. Veenstra.

KIMERIDGIAN PLIOSAUR SPECIES

1. *Pleiosaurus aequalis* Phillips, 1871.
2. *Polyptychodon archiaci* Deslongchamps, no date (?1872).
3. *PLIOSAURUS BRACHYDEIRUS* Owen, 1841.
4. *PLIOSAURUS BRACHYSPONDYLUS* (Owen), 1839.
5. *Spondylosaurus frearsi* Fischer de Waldheim, 1845.
6. *Plesiosaurus giganteus* Conybeare, 1824*a*.
7. *Plesiosaurus grandis* Owen, 1839.
8. *Peloneustes irgisensis* Novozhilov, 1948.
9. *STRETOSAURUS MACROMERUS* (Phillips), 1871.
10. *Pleiosaurus nitidus* Phillips, 1871.
11. *Pliosaurus planus* Hulke, 1883.
12. *Pliosaurus portlandicus* Owen, 1869.
13. *Plesiosaurus recentior* Parkinson, 1822.
14. *Pliosaurus rossicus* Novozhilov, 1948.
15. *Polycotylus suprajurensis* Sauvage, 1876.
16. *Pliosaurus suprajurensis* Sauvage, 1879.
17. *Pleiosaurus simplex* Phillips, 1871.
18. *Plesiosaurus sterrodeirus* Seeley, 1869.
19. *Plesiosaurus trochanterius* Owen, 1839.
20. *Pliosaurus wosinskii* Fischer de Waldheim, 1846.

OXFORDIAN PLIOSAUR SPECIES

21. *PLIOSAURUS ANDREWSI* sp. nov.
22. *Thaumatosaurus calloviensis* Bogolubov, 1912.
23. *Pliosaurus evansi* Seeley, 1869.
24. *LIOPLEURODON FEROX* Sauvage, 1873.
25. *Pleiosaurus gamma* Phillips, 1871.
26. *Pliosaurus giganteus* Wagner, 1852.
27. *Pliosaurus giganteus* Trautschold, 1860.
28. *Liopleurodon grossouvrei* Sauvage, 1873.
29. *Ischyrodon meriani* Meyer, 1856*a*.
30. *Thaumatosaurus mosquensis* Kiprijanoff, 1883.
31. *SIMOLESTES NOWACKIANUS* Huene, 1938.
32. *Thaumatosaurus oolithicus* Meyer, 1841.
33. *LIOPLEURODON PACHYDEIRUS* (Seeley), 1869.
34. *PELONEUSTES PHILARCHUS* (Seeley), 1869.
35. *SIMOLESTES VORAX* Andrews, 1909.
36. *Sinopliosaurus weiyuanensis* Young, 1942.

N.B. The species shown in large type are here described in detail as they are considered valid.

II. SYSTEMATIC DESCRIPTIONS

Family PLIOSAURIDAE

DIAGNOSIS. Head large, tending to be long and slender; irregular dentition with large caniniform teeth. Neck short, approximately 22 cervical vertebrae, centra short; cervical ribs double-headed. Coracoids and ischia elongated. Propodials relatively long and slender, compressed dorso-ventrally and expanded distally; humerus shorter than femur.

1. *Kimeridgian Forms*

Genus ***PLIOSAURUS*** Owen, 1841

EMENDED DIAGNOSIS. Mandible with long symphysis bearing 10–12 pairs of teeth of which the anterior 5–6 are large and caniniform; total of 30–38 teeth in each ramus. Cervical vertebrae short, length about half width or height; cervical ribs double-headed. Scapula triradiate with dorsal process directed laterally and ventral plate expanded medially.

TYPE SPECIES: *Pliosaurus brachydeirus* Owen.

Pliosaurus brachydeirus Owen

(Pl. 20; Text-figs. 3–5)

1824*a*. *Plesiosaurus giganteus* Conybeare, p. 389.
1841. *Pleiosaurus brachydeirus* Owen, pp. 282–285, pl. 68, fig. 5; pl. 72, fig. 5.
1841*a*. *Pleiosaurus brachydeirus* Owen: Owen, pp. 60–65.
1869. *Pliosaurus brachydeirus* Owen: Owen, p. 6.
1869. *Plesiosaurus sterrodeirus* Seeley, p. 98.
1871. *Pleiosaurus brachydeirus* Owen: Phillips, pp. 341–354, text-figs. 134–141, 146, 147, 160.
1879. *Pliosaurus suprajurensis* Sauvage, pp. 12–13, pl. 27, fig. 1.
1889*a*. *Pliosaurus brachydirus* Owen: Lydekker, p. 50.
1889*b*. *Pliosaurus brachydirus* Owen: Lydekker, pp. 120–128, text-figs. 36–38.
1959. *Pliosaurus brachydeirus* Owen: Delair, pp. 69–70.
1959. *Pliosaurus brachydeirus* Owen: Tarlo, pp. 286, 290.
1959*a*. *Pliosaurus brachydeirus* Owen: Tarlo, pp. 52–53.

EMENDED DIAGNOSIS. Teeth trihedral in cross-section, outer surface smooth and flat. Cervical vertebrae with well-marked ventral keel; posterior cervical vertebrae with boss in centre of articular surface. Epipodials short.

MATERIAL. Holotype, J.9245 A, B; J.9285; J.9292–9298; etc.; University Museum, Oxford; teeth, lower and upper jaws, vertebral column, femur, tibia, fibula; Kimeridge Clay, Market Rasen, Lincolnshire, described Owen (1841*a*), figured Phillips (1871).

HISTORY OF THE SPECIES. Conybeare (1824*a*) erected the name *Plesiosaurus giganteus* to cover all plesiosaurians with shortened neck vertebrae, and included in this species the pliosaur skeleton from Market Rasen, although no description of it was given. Later, Owen (1841) described the teeth and jaws of this specimen as representing a new genus and species for which he proposed the name *Pleiosaurus brachydeirus*. The same year (1841*a*) he added a description of the vertebrae and limb bones still using the name *P. brachydeirus*, and suggested that *Plesiosaurus grandis* and *P. trochanterius* be included in the genus *Pliosaurus*.

In 1861, however, he erroneously claimed *P. grandis* as the type species of *Pliosaurus*, making *P. brachydeirus* a synonym of *P. grandis* (with the proviso in 1869 that the name *P. brachydeirus* be retained for the Market Rasen specimen). Phillips in 1871 figured the Market Rasen pliosaur under the name *P. brachydeirus*, recognizing that this was the type species. Lydekker (1889*a*, *b*) also correctly accepted *P. brachydeirus* as the type species.

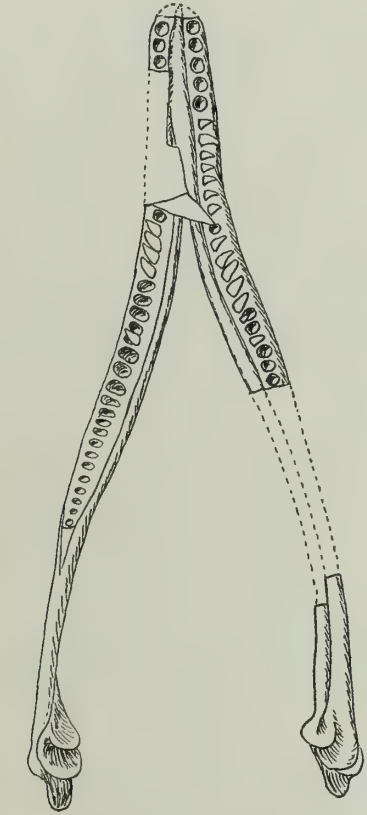


FIG. 3. *Pliosaurus brachydeirus* Owen, holotype Univ. Mus. Oxf. Mandible in dorsal view, $\times\frac{1}{10}$. After Phillips (1871).

Lydekker (1889*a* : 50) considered that there were 12 pairs of teeth included in the mandibular symphysis of *P. brachydeirus*, but later (1889*b* : 120, 123) he modified his view and claimed that the symphysis only extended back to the 7th pair of teeth, the apparent length of the symphysis being due to lateral crushing. Lydekker's second view, since it appeared in the *Catalogue of Fossil Reptiles* has tended to become established, and a mandible with only 7 pairs of teeth in the symphysis is generally considered to be a diagnostic feature of the genus *Pliosaurus* (see Andrews, 1913; Delair, 1959). In a recent diagnosis of the genus *Pliosaurus* (Tarlo, 1959), it was claimed that 10–12 pairs of teeth in the mandibular symphysis is characteristic of the genus and in particular of the Market Rasen jaw, and the figure of the symphysial region of the mandible (Pl. 20, fig. 1) shows that there must in fact have been 10–12 pairs of teeth. A detailed description of the holotype is given below from which it is hoped that the true diagnostic features of the genus *Pliosaurus* can be established.

DESCRIPTION OF HOLOTYPE. *Teeth.* Owen (1841, pl. 68, fig. 5; pl. 72, fig. 5) figured the crown of a tooth belonging to the Market Rasen pliosaur. This tooth was sub-trihedral in cross-section; the enamel of the crown was ornamented by longitudinal ridges; the outer surface of the crown was smooth, being devoid of ridges. This flat outer surface was delimited by two strong ridges at either side, often termed carinae. (*N.B.* As all Kimeridgian pliosaurs so far described have such teeth they cannot be used to distinguish Kimeridgian species from one another.)

Mandible. The mandible (Text-fig. 3) is incomplete in the region of the symphysis and the middle portion of the right ramus is missing. The right ramus is complete up to the 12th tooth, and the left from the 12th or 13th to the 37th or 38th. It thus appears that there were 37–38 teeth in each ramus of the mandible. The three alveoli which are preserved in the anterior part of the left ramus suggest that this part of the symphysis was expanded. On the right side there are 5–7 large caniniform teeth present with their crowns missing. Posterior to these teeth are six smaller ones, all of which, with the possible exception of the last, were included in the symphysis. It appears therefore that there were 10–11 pairs of teeth in the symphysis, of which the anterior 5–7 were large and caniniform.

Vertebral column. The known vertebrae include ten cervical, twelve dorsal and one caudal. Six of the dorsal vertebrae are preserved in natural articulation with a number of fragmentary ribs and isolated teeth adhering to them. The serial position of the cervical centra can be ascertained from the fact that their length increases down the neck.

Cervical vertebrae. Five cervical vertebrae only are considered here, since the others are not well preserved. Their measurements in mm. are given in the table below:

Anterior cervical centra	Length	Width	Height
J.9292	40	88	75
J.9293	40	90	83
J.9294	42	92	85
Posterior cervical centra			
J.9297	46	110	90
J.9298	48	103	83

Anterior cervical vertebrae. The anterior articular surface is circular in outline and concave, with the margin bevelled and bordered by a narrow peripheral groove.

The margin of the posterior articular surface is bevelled in three places—between the inferior rib facets, and on either side between the superior rib facets and the base of the neural arch. On the lateral surface there are double rib facets; the inferior facet is oval in outline (antero-posteriorly) and the superior facet tends to be triangular with a faint ridge extending from its apex to the base of the neural arch. On the ventral surface there is a strongly developed ventral keel in the mid-line, with a depression on either side. There is no suggestion of rugosity along the anterior and posterior margins.

Posterior cervical vertebrae. These centra are characterized by a large convex boss in the centre of their articular faces. The superior rib facets are larger than in the anterior cervicals and the inferior facets have usually disappeared, but specimen J.9298 has a single rib facet on its left side and a double one on the right. On the ventral surface there is no longer a ventral keel, but the centrum is strongly convex from side to side.

Dorsal vertebrae. In this part of the vertebral column the ribs are borne on the transverse processes of the neural arch, and the centra are more or less cylindrical in shape but somewhat resemble a shallow pulley. Unfortunately they have no characters of diagnostic value and are useless for identification.

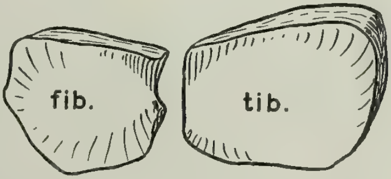


FIG. 4. *Pliosaurus brachydeirus* Owen, holotype. Epipodials of hind limb, $\times\frac{1}{5}$. fib., fibula; tib., tibia.

Caudal vertebrae. Only one centrum is known from the tail region; it has single rib facets, and, on its anterior and posterior ventral margins, four characteristic chevron bone facets.

Limb bones. Owen (1841*a*) described two femora with different measurements in his account of the Market Rasen skeleton, but Phillips (1871) considered the smaller of the two bones to be the humerus. However, from an examination of the material, only the femur J.9285 can definitely be assigned to the type skeleton, the other probably belonging to a different animal. The length of the femur is 658 mm. and its proportions can be seen from Pl. 20, fig. 3. Preserved together with a number of tarsal bones are the tibia and fibula of the same limb as the femur (see Text-fig. 4). These two bones are of special interest as they are both much shorter than wide. Such short epipodials have previously been considered characteristic of the Cretaceous Polycotylids, so that their presence in the type of *Pliosaurus* necessitates a revision of the diagnosis of both the Pliosauridae and the Polycotylidae.

Scapula of Pliosaurus. No parts of the limb girdles of *P. brachydeirus* are known, but in order to give a full account in one place of the diagnostic features of the genus *Pliosaurus*, a description of a scapulae of the kind belonging to *Pliosaurus brachyspondylus* is given below. This type of scapula is a triradiate bone with a strong, thickened, glenoid ramus which bears a facet for the articulation of the coracoid, and another which forms the anterior part of the glenoid cavity. Medially the scapula thins out and is expanded into a broad flat sheet termed the ventral plate. Laterally there is a further extension—the dorsal process which is approximately the same width as the glenoid ramus and which again forms a thin sheet. The dorsal process projects either laterally or postero-laterally and in ventral view is set off at an angle to the plane of the bone, from a ridge which extends to the anterior point of the ventral plate from the glenoid cavity. Immature scapulae of a similar kind are also known (Lydekker, 1889*b* : 122) but there is no way of ascertaining their specific identity. They clearly belong to *Pliosaurus* and they are of interest as they show how the proportions of the three processes of the scapula changed as the animal approached maturity. These changes can best be appreciated by comparing the immature and mature scapulae shown in Text-fig. 5.

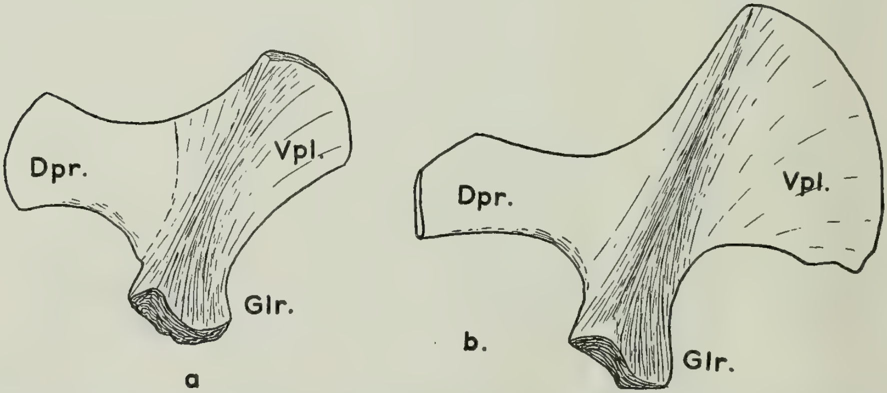


Fig. 5. *Pliosaurus* sp. Scapulae in ventral view. *a.* Immature right scapula (31934, B.M. (N.H.)) × $\frac{1}{5}$; *b.* Adult right scapula (R.287 B.M. (N.H.)) × $\frac{1}{8}$; Dpr., dorsal process ; Glr., glenoid ramus ; Vpl., ventral plate.

Pliosaurus brachyspondylus (Owen)

(Pl. 21 ; Text-fig. 6)

1822. *Plesiosaurus recentior* Parkinson, pp. 295–298.
1824*a*. *Plesiosaurus giganteus* Conybeare, p. 389.
1839. *Plesiosaurus brachyspondylus* Owen, pp. 78–80.
1845. *Plesiosaurus brachyspondylus* Owen : Owen, p. 417.
1845. *Spondylosaurus frearsi* Fischer de Waldheim, pp. 343–351, pls. 7, 8.
1846. *Pliosaurus wosinskii* Fischer de Waldheim, pp. 90–107, pls. 3, 4.
1868. *Pliosaurus brachyspondylus* (Owen) Eichwald, pp. 1280–1281.

1869. *Pliosaurus brachyspondylus* (Owen) : Seeley, pp. 97, 102–104.
1871. *Pleiosaurus nitidus* Phillips, pp. 360–361, text-figs. 156–158.
1889*b*. *Pliosaurus brachyspondylus* (Owen) : Lydekker, pp. 139–140.
1959. *Pliosaurus brachyspondylus* (Owen) : Tarlo, pp. 283–291, text-figs. 1, 2, pls. 51, 52.
1959. *Pliosaurus brachyspondylus* (Owen) : Delair, pp. 70–71.

EMENDED DIAGNOSIS. Teeth trihedral in cross-section, outer surface smooth and flat. Cervical vertebrae with finely sculptured double rugosity on ventral surface and no ventral keel; posterior cervical vertebrae with no boss in centre of articular surfaces.

MATERIAL. Proposed Neotype, J.29564, Sedgwick Museum, Cambridge; posterior cervical centrum; Kimeridge Clay, Ely, Cambridgeshire; described Seeley (1869 : 97, 103), figured Tarlo (1959, pl. 51, figs. 1–1*c*). For list of other material, see Tarlo (1959).

HISTORY OF THE SPECIES. In 1822 Conybeare read a paper (1824) to the Geological Society of London in which he figured several pliosaur neck vertebrae from the Kimeridge Clay of Weymouth. Also in 1822, Parkinson assigned all such vertebrae to the species *Plesiosaurus recentior*. Conybeare later (1824*a*) proposed the name *Plesiosaurus giganteus* for plesiosaurians with shortened neck vertebrae and included the remains from Weymouth in this species. Owen (1839) also described such shortened cervical vertebrae from the Kimeridge Clay of the Headington Pits near Oxford, but proposed the name *Plesiosaurus brachyspondylus* for them and also for the vertebrae from Weymouth. This specific name was in fact the first that could be considered valid since it was accompanied by an adequate description. He later (1845) identified a cervical centrum from the Kimeridge Clay of Moscow as belonging to the same species, although Fischer de Waldheim (1845) made it the type of the species *Spondylosaurus frearsi*. Unfortunately the specimens from Headington, formerly in the collection of Viscount Cole (later Earl of Enniskillen) can no longer be traced, and those from Weymouth were destroyed during the bombing of Bristol in November 1940 (Swinton, 1948; Delair, 1959).

Seeley (1869) was the only other author to discuss the species *Plesiosaurus brachyspondylus* which he correctly assigned to the genus *Pliosaurus*, following Eichwald (1868). In his paper Seeley described a posterior cervical centrum from the Kimeridge Clay of Roswell Pit, near Ely, as *Pliosaurus brachyspondylus* and this specimen has recently been proposed as the neotype (Tarlo, 1959).

It should be noted that Phillips (1871) described and figured several plesiosaur vertebrae and incorrectly assigned them to *Plesiosaurus brachyspondylus* Owen. In the same work he figured a posterior cervical centrum which he named *Pleiosaurus nitidus*. This specimen is now lost but Lydekker (1889*b*) claimed that it closely accorded with the posterior cervical centrum described by Seeley (1869) as belonging to *P. brachyspondylus*. Phillips' figure supports Lydekker's view and thus *P. nitidus* is here included as a synonym of *P. brachyspondylus*.

In 1889 a pliosaur skeleton was discovered in the Kimeridge Clay of Roswell Pit near Ely, and it has been recently described and figured (Tarlo, 1959) under the name *Pliosaurus brachyspondylus* (Owen). This pliosaur skeleton is the most complete of any from the Kimeridge Clay. This species, which was formerly one of the most obscure, is now the best known of Kimeridgian pliosaurs.

Description of proposed neotype. The neotype centrum is very distinctive as it possesses a double rib facet on its left side and a single facet on the right. The articular surfaces of the vertebra are transversely ovate in outline and are slightly concave. Each has a small depression at its centre, without any suggestion of convexity here as in the posterior cervical vertebrae of other Kimeridgian pliosaur species. The margins of the articular surfaces are very sharply defined, and there is no evidence of either a marginal bevel or groove. On the anterior and posterior margins of the ventral surface of the centrum are two strips of finely sculptured rugose bone between which the surface is remarkably smooth. This last feature is very striking and can readily be used to distinguish the species.

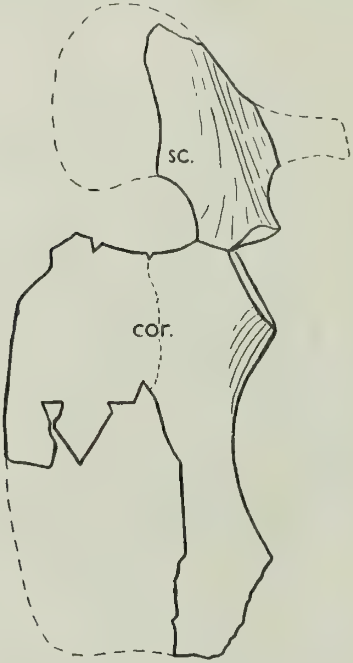


Fig. 6. *Pliosaurus brachyspondylus* (Owen). J.35991, Sedgwick Mus. Reconstruction of left half of pectoral girdle, × 1/8. After Tarlo (1959.)

Description of associated skeleton from Ely. *Teeth.* The teeth are similar to those of *Pliosaurus brachydeirus* Owen, being trihedral in cross-section ; the enamel of the flat outer surface is smooth but the remainder of the crown is characterized by longitudinal ridges.

Mandible. The symphysial portion of the mandible contains 10 teeth on each side, of which the anterior six are large and caniniform. There are 30 teeth in the right ramus and 31 in the left. This specimen is similar in shape to the mandible of *P. brachydeirus.*

Cervical vertebrae. The first cervical vertebra posterior to the atlas-axis has a pronounced ventral lip directed anteriorly with a marked rugose area behind it on the ventral surface of the centrum, which tends to produce a faint ventral keel. However, in the majority of the cervical vertebrae, there is no suggestion of such a keel, and the rugosities on their ventral surfaces are limited to strips along the anterior and posterior margins. There are double rib facets on the lateral surfaces of the centra of all the anterior cervical vertebrae, the inferior facet in each case being more or less circular in outline, while the superior facet tends to be triangular with a narrow ridge extending from its apex to the base of the neural arch. The articular surfaces of the anterior cervicals show a well-developed marginal bevel, but this disappears in the posterior cervicals. The articular surfaces are also slightly concave and have a small central pit, no mamilla being developed as in other Kimeridgian species.

The four most posterior of the cervical centra can be distinguished from the anterior cervicals because they have single rib facets, and the bevelling of the margins of their articular surfaces is slight. The articular surfaces are slightly concave and each has a depression in the centre, but the boss usually found in Kimeridgian species is absent. In other respects the posterior cervical vertebrae resemble the anterior cervicals.

Scapula. Sufficient of the left scapula is preserved in one piece on the ventral surface of a series of vertebrae to show that it is of the same kind as that described above under *P. brachydeirus*, and a reconstruction of this bone is given in Text-fig. 6 together with that of the coracoid.

Propodials. The humerus is completely preserved and is indistinguishable from the propodials of most other pliosaurs. The left femur is also preserved whole with a number of phalanges adhering to it. This bone although larger is very similar to the humerus in its proportions.

Epipodials. No epipodials are known from this skeleton.

Genus ***STRETOSAURUS*** Tarlo, 1959

DIAGNOSIS. Mandible with short symphysis bearing 5–6 pairs of large caniniform teeth ; total of approximately 24–26 teeth in each ramus. Teeth trihedral in cross-section, outer surface smooth and flat. Cervical vertebrae short, length less than half width or height. ventral keel absent ; posterior cervical vertebrae with rib facets borne on pedicle and boss in centre of articular surfaces. Caudal vertebrae with no chevron bone facets. Scapula triradiate with dorsal process produced anteriorly and ventral plate little expanded. Epipodials short.

TYPE SPECIES : *Stretosaurus macromerus* (Phillips)

Stretosaurus macromerus (Phillips)

(Pl. 22; Text-figs. 7, 8)

1869. *Pliosaurus grandis* (Owen): Owen, pp. 1–6, pls. 1, 2.
1869*a*. *Pliosaurus grandis* (Owen): Owen, pp. 152–153, pl. 18.
1869. *Pliosaurus brachydeirus* Owen: Seeley, pp. 102–104.
1869. *Pliosaurus grandis* (Owen): P. Fischer, pp. 253–269, pl. 15.
1871. *Pleiosaurus macromerus* Phillips, pp. 354–358, text-figs. 148, 151, 159.
1872?. *Polyptychodon archiaci* Deslongchamps, pp. 30–35, pl. 5, figs. 1, 2; pl. 11, figs. 5, 6.
1889*b*. *Pliosaurus macromerus* Phillips: Lydekker, pp. 131–139, text-figs. 41–43.
1947. *Pliosaurus* cf. *grandis* (Owen): Rozhdestvensky, pp. 197–199, text-figs. 1, 2.
1958*a*. *Pliosaurus macromerus* Phillips: Tarlo, pp. 193–199, text-figs. 1*c*, 2*b* 3, 4; pls. 36, 37.
1959. *Pliosaurus macromerus* Phillips: Delair, pp. 71–72.
1959*a*. *Stretosaurus macromerus* (Phillips) Tarlo, pp. 39–55, text-figs. 1–6, pls. 7–9.

DIAGNOSIS. As for genus (only species).

MATERIAL. Lectotype, J.10441, University Museum, Oxford; anterior cervical centrum; Kimeridge Clay, Shotover Railway Cutting, Oxfordshire. Figured Phillips (1871, fig. 148), Tarlo (1959*a*, pl. 8, figs. 1–1*b*). For other material see Tarlo (1959*a*).

HISTORY OF THE SPECIES. Owen described and figured a cervical centrum from the Kimeridge Clay of Foxcombe Hill, near Oxford, under the name *Pliosaurus grandis* (1869*a*: 152–158, pl. 18, figs. 1, 2). This specimen accords with the lectotype of *Stretosaurus macromerus* (Phillips) being notable for the absence of a ventral keel. At the same time Owen (1869) also described and figured a large mandible from the Kimeridge Clay of Kimeridge Bay as *P. grandis*. Its mandible contained 25–26 pairs of teeth of which the anterior six pairs were large and caniniform, these forming the full complement of teeth in the symphysis. P. Fischer (1869) described and figured a similar type of mandible from the Kimeridge Clay of Le Havre. Deslongchamps (?1872), described the same specimen under the name *Polyptychodon archiaci*, but his figures are the mirror-images of those of P. Fischer. Recently a similar mandible of giant size from the Kimeridge Clay of Cumnor was described and figured (Tarlo, 1959*a*) when all Kimeridgian mandibles with this comparatively short mandibular symphysis were provisionally assigned to *Stretosaurus macromerus*.

Seeley (1869) described some posterior cervical vertebrae under the name *Pliosaurus brachydeirus* and these have recently been referred to *S. macromerus* (see Tarlo, 1959*a*). Phillips (1871) erected the name *Pleiosaurus macromerus* to cover a miscellaneous collection of vertebrae and a large propodial bone. The anterior cervical centrum which he figured (fig. 148) has been chosen as the lectotype. Lydekker (1889*b*) placed most pliosaur remains of large size in *P. macromerus* including the mandible described by Owen (1869). Tarlo (1958*a*) described the scapula of *P. macromerus* and later (1959*a*) claimed that the pectoral girdle was sufficiently distinct from that of *Pliosaurus* to warrant the erection of the new genus *Stretosaurus*.

It should be noted, however, that although Kuhn (1935) lists "*Plesiosaurus macromerus* Giebel, 1847" in his synonymy of the species this is actually incorrect as Giebel (1847) listed Owen's species *Plesiosaurus macromus* which is in no way connected with *S. macromerus*.

DESCRIPTION OF LECTOTYPE. The lateral surface of the lectotype centrum bears two rib facets which are oval in outline, their long axes being directed anteroposteriorly. In this specimen the superior facet is smaller than the inferior. The lateral surface between the base of the neural arch and the superior rib facet is quite smooth with no suggestion of a ridge. The anterior articular surface is concave with a poorly developed mamilla at the centre ; the outline of the centrum is circular with a well-marked peripheral groove. The posterior articular surface is also concave and somewhat circular in outline, with its margin bevelled along the ventral edge and also between the base of the neural arch and the top of the rib facets. The

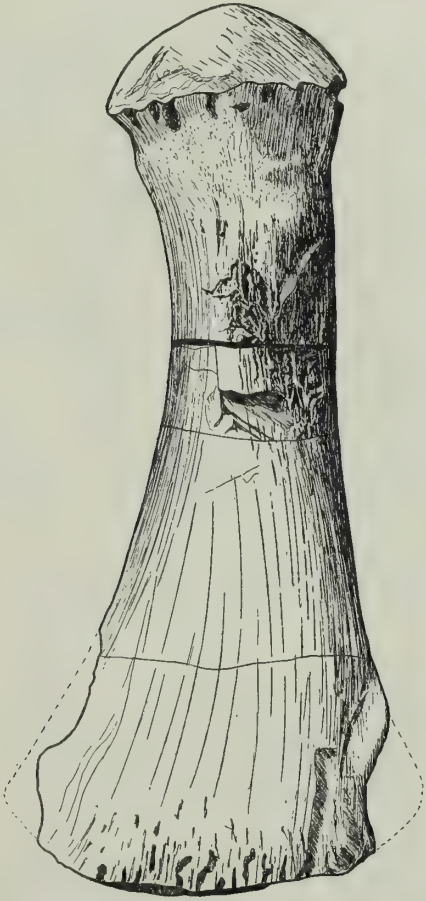


FIG. 7. *Stretosaurus macromerus* (Phillips). J.35990, Sedgwick Mus. Left femur in ventral view, × $\frac{1}{8}$.

anterior and posterior margins of the ventral surface of the centrum are somewhat roughened ; there is no evidence of a ventral keel.

Description of associated skeleton from Stretham. *Teeth.* The teeth are similar to those of *Pliosaurus brachydeirus* Owen, being trihedral in cross-section ; the enamel of the flat outer surface is smooth but the remainder of the crown is characterized by longitudinal ridges.

Cervical vertebrae. The ventral surface of the four known anterior cervical vertebrae is flat with no suggestion of a ventral keel ; the lateral surface of the centra between the superior rib facet and the neural arch is smooth with no indication of a ridge. In the centre of each articular surface a small mamilla is found punctured by a nutritive foramen. Three centra are known from the posterior part of the neck. All have a large rounded boss in the centre of their articular surfaces, and compared with the anterior cervicals the first two specimens show a marked reduction of the inferior rib facets. In the last posterior cervical centrum only a single rib facet remains. this being borne on a pedicle situated on the upper half of the lateral surface of the centrum. A sharp ridge is developed between the dorsal edge of this pedicle and the base of the neural arch, the suture line of which extends laterally towards the rib facet.

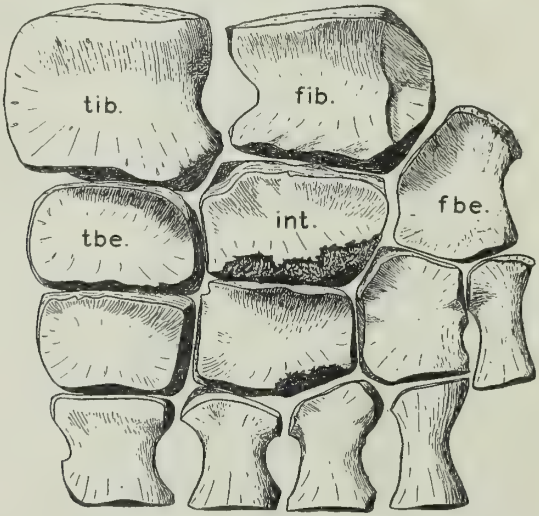


Fig. 8. *Stretosaurus macromerus* (Phillips). J.35990, Sedgwick Mus. Epipodials and tarsus of left hind limb, in dorsal view, ×$\frac{1}{6}$. tib., tibia ; fib., fibula ; tbe., tibiale ; int., intermedium ; fbe., fibulare.

Scapula. The scapula is a triradiate bone in which the whole surface is in one plane, no part being set off at an angle. The glenoid ramus is thickened and elongated, the ventral plate is not greatly expanded, and the dorsal process is produced anteriorly and does not project laterally. By the anterior production of the dorsal process of the scapula the pre-glenoid length of the whole pectoral girdle is greatly increased. A pectoral girdle containing the type of scapula described above is different from that of any previously known pliosaur, and for this reason the new genus *Stretosaurus* was proposed.

Propodials. The head of the humerus is more massive than that of the femur although the humerus is, on the whole, a smaller bone with a very slender shaft ; the femur has more normal proportions (see Text-fig. 7).

Epipodials. These are short as in *Pliosaurus brachydeirus* (Text-fig. 8).

DESCRIPTION OF MANDIBLE OF *Stretosaurus*. No mandible is known from *Stretosaurus macromerus*, but a description is given below of the kind of mandible generally assigned to this species. There are usually 25 pairs of teeth in the mandible, but only the anterior 6–7 pairs, which are large and caniniform, are included in the symphysis. This type of mandible contrasts with that of *Pliosaurus* where there are 10–12 pairs of teeth in the symphysial portion.

2. *Oxfordian Forms*

Genus ***PLIOSAURUS*** Owen, 1841

Pliosaurus andrewsi sp. nov.

(Pl. 23 ; Pl. 28 ; figs. 4–4*b*)

1871. *Pleiosaurus ? grandis* (Owen) : Phillips, p. 318, text-fig. 122.
1889*b*. *Pliosaurus evansi* Seeley : Lydekker, p. 129.
1889*b*. *Pliosaurus grossouvrei* (Sauvage) Lydekker, pp. 130–131, text-fig. 40.
1889*b*. *Peloneustes philarchus* (Seeley) : Lydekker, p. 154.
1890. *Peloneustes evansi* (Seeley) Lydekker, pp. 49–52.
1890*a*. *Peloneustes evansi* (Seeley) : Lydekker, p. 273.
1913. *Peloneustes evansi* (Seeley) : Andrews, pp. 71–79, text-figs. 6B, 27B, 28–30.
1946. ?*Sinopliosaurus weiyuanensis* Young : Young, pp. 203–205, pl. 2, fig. 3*b*.
1958. *Pliosaurus* sp. nov. Tarlo, pp. 439–441.

DIAGNOSIS. Teeth circular in cross-section ; enamel smooth with few fine ridges mainly confined to inner surface of crown. Cervical vertebrae generally have no ventral keel ; no finely sculptured double rugosities present on ventral surface. Epipodials long.

MATERIAL. Holotype, R.3891, British Museum (Nat. Hist.), associated skeleton, Oxford Clay, Peterborough, figured Andrews (1913).

HISTORY OF THE SPECIES. Phillips (1871) figured a mandible from the Oxford Clay of Eyebury, under the name *Pleiosaurus ?grandis*. As this specimen has a mandibular symphysis containing 11 pairs of teeth, of which the anterior 5–6 are large and caniniform, Lydekker (1889a) referred it to *Peloneustes philarchus* (Seeley). At the same time he described a number of teeth of Corallian age under the name *Pliosaurus grossouvrei* (Sauvage) commenting that they might in fact belong to

P. evansi. Lydekker (1890, 1890*a*) included the same mandible in *Peloneustes evansi* (Seeley). In 1913 Andrews described an associated pliosaur skeleton under the name *Peloneustes evansi* which had a similar mandible, and since the mandible of this species is much like that of *Pliosaurus brachydeirus* (the type species) it should be placed within the genus *Pliosaurus.* However, the material described by Lydekker and Andrews as *P. evansi* is unlike Seeley's type of this species (which in any case is now included in the synonymy of *Peloneustes philarchus*) and a new species *Pliosaurus andrewsi* is here proposed for this material. The skeleton described by Andrews is chosen as the holotype of this new species. Young (1946) described several teeth which he referred to *Sinopliosaurus weiyuanensis,* but from their description they appear to be conspecific with *P. andrewsi.*

DESCRIPTION OF HOLOTYPE. *Teeth.* The teeth are circular in cross-section ; the enamel of the crown is generally smooth, the few enamel ridges being confined to the inner surfaces. This pattern of ornamentation is very distinctive and enables the species to be recognized from isolated teeth. A feature of the teeth of this species, noted by Andrews, is that they undergo wear to a greater extent than in any other plesiosaurian.

Mandible. Unlike the mandible figured by Phillips (1871), the specimen has been crushed laterally. The slight angle in the two rami (at the 12th tooth) marks the end of the symphysis which contained 12 pairs of teeth, the anterior seven of which were large and caniniform. The total number of teeth in each ramus was about 32. This mandible is very similar to that of *P. brachydeirus.*

Vertebral column. The entire vertebral column is preserved, but as the dorsal and caudal vertebrae add little to our knowledge their description is omitted. The cervical vertebrae are, however, of critical importance, as it was by means of their characters only that this skeleton was incorrectly placed in the species *Peloneustes evansi* by Andrews.

Cervical vertebrae. The articular surfaces are circular in outline with a narrow peripheral groove. In this skeleton the double-headed cervical ribs are preserved in natural articulation. The most important feature of these vertebrae is, however, the complete absence of a ventral keel, quite unlike the type specimen of *P. evansi* (now referred to *Peloneustes philarchus*) in which the ventral keel is strongly developed. On the lateral surface of the centra there is no ridge between the superior rib facet and the base of the neural arch. One of the posterior cervical centra is of interest since it exhibits a double rib facet on the left side and a single one on the right. Isolated vertebrae of this species are virtually indistinguishable from those of *Simolestes vorax* Andrews.

Propodials. Both hind and fore limbs are preserved. The humerus is shorter and broader than the femur.

Epipodials. The tibia, fibula and ulna are greater in length than in width ; in the radius, however, these proportions are reversed.

Scapula of P. andrewsi. There is no scapula associated with the holotype but the skeleton (R.2437) which can be referred to *Pliosaurus andrewsi* contains a scapula. It is similar to that described under *P. brachydeirus,* except that the dorsal process is somewhat expanded distally (see Pl. 23, fig. 1).

Genus ***LIOPLEURODON*** Sauvage, 1873

Emended diagnosis. Mandible with short symphysis bearing 5–7 pairs of large caniniform teeth ; total of about 25–28 teeth in each ramus. Teeth circular in cross-section ; fewer longitudinal ridges on outer surface of crown than on inner surface. Cervical vertebrae short, length half or less than half of width or height. Scapula triradiate with dorsal process directed laterally and ventral plate expanded medially. Epipodials long.

Type species : *Liopleurodon ferox* Sauvage.

Liopleurodon ferox Sauvage

(Pl. 24 ; Pl. 28, figs. 2–2*b*)

1852. *Pliosaurus giganteus* Wagner, pp. 663–710, pl. 20.
1856.*a* *?Ischyrodon meriani* von Meyer, pp. 19–21, pl. 2, figs. 1–4.
1860. *Pliosaurus giganteus* Trautschold, p. 356, pl. 8, fig. 25.
1873. *Liopleurodon ferox* Sauvage, pp. 378–379, pl. 7, fig. 1.
1880. *Polyptychodon ferox* (Sauvage) Sauvage, p. 544.
1883. *Thaumatosaurus mosquensis* Kiprijanoff, p. 27, pl. 14, fig. 1.
1888. *Pliosaurus ferox* (Sauvage) Lydekker, p. 353.
1889*b*. *Pliosaurus ferox* (Sauvage) : Lydekker, pp. 145–147, text-fig. 45.
1897. *Pliosaurus ferox* (Sauvage) : Andrews, pp. 177–183, pl. 12.
1905. *Liopleurodon ferox* Sauvage : Blake, pp. 23–25.
1911. *Pliosaurus* (*Liopleurodon*) cf. *ferox* (Sauvage) : Bogolubov, pp. 153–154.
1912. *Liopleurodon ferox* Sauvage : Bogolubov, p. 5.
1913. *Pliosaurus ferox* (Sauvage) : Andrews, pp. 2–23, text-figs. 2, 3, 7 ; pls. 1, 2.
1934. *Pliosaurus ferox* (Sauvage) : von Huene, pp. 31–46, text-figs. 1–26.
1939. *Pliosaurus* cf. *ferox* (Sauvage) : Bigot, pp. 635–636, pl. 37 *bis*.
1944. *Pliosaurus ferox* (Sauvage) : Gross, pp. 227–230, text-figs. 1–3.

Emended diagnosis. Teeth with ornamentation of well-spaced coarse ridges on inner surface, and few widely and unevenly spaced ridges on outer surface between which are wide smooth areas. Cervical vertebrae with length less than half width or height ; ventral lip developed on anterior surface of centrum, ventral keel absent.

Material. Holotype, a tooth from the Oxford Clay of Wast near Boulogne. Associated skeleton (R.3536) from the Oxford Clay of Peterborough.

History of the species. In 1852, Wagner described and figured a tooth from the Oxfordian of Bavaria under the name *Pliosaurus giganteus* ; this tooth was circular in cross-section, and thus differed from all other pliosaur remains described at that time (with the exception of *Thaumatosaurus oolithicus* Meyer). Unfortunately Wagner's trivial name had been used by Conybeare (1824*a*) for pliosaur remains which he named *Plesiosaurus giganteus*. Meyer (1856*a*) described and figured a further tooth of Oxfordian age with a circular cross-section to which he gave the name *Ischyrodon meriani*. (He had erected this name in 1838, but it remained a *nomen nudum* until 1856*a*.) Although this tooth has generally been included in the synonymy of the Kimeridgian *S. macromerus* (see Lydekker, 1889*b* ; Delair, 1959), it is suggested here that it may belong to *L. ferox* Sauvage. It is not certain from Meyer's figure whether this assignment is altogether justified, but it is closer to *L. ferox* than to any other species and is therefore tentatively included in its synonymy. Trautschold (1860) described and figured a small tooth of Oxfordian age under the preoccupied name of *Pliosaurus giganteus*.

Sauvage (1873) described a tooth from the Oxford Clay of Wast near Boulogne-sur-Mer, which he made the type of *Liopleurodon ferox*. In 1880 he transferred this species to the genus *Polyptychodon*. Lydekker (1888) referred the species to *Pliosaurus* and described some Oxfordian pliosaur remains under the name *Pliosaurus ferox*. These are referred below to *Liopleurodon pachydeirus* (Seeley).

Blake (1905) discussed the generic name, arguing for the retention of Sauvage's name *Liopleurodon*. Bogolubov (1911) retained it, but only as a subgenus of *Pliosaurus*; but later (1912), he too accepted *Liopleurodon* as the generic name for *L. ferox*. All subsequent authors have taken *Liopleurodon* to be a synonym of *Pliosaurus* (Andrews, 1913; Linder, 1913; Delair, 1959). It is clear, however, that *L. ferox*, which has a mandible with a short symphysis containing 6–7 pairs of large caniniform teeth is distinct from *Pliosaurus*, and should be generically distinguished from it. For this reason I have followed Blake and resurrected Sauvage's original generic name *Liopleurodon*. The re-description given below is based on the associated skeleton (R.3536) which has teeth identical in character with the holotype. It is considered necessary to include it here as even Andrews' excellent description of this species (1913) suffered from the inclusion of material which I have felt obliged to transfer to *L. pachydeirus* (Seeley). The skeleton described as *Pliosaurus ferox* by von Huene (1934) is retained in that species on the characters of its teeth. The teeth described by Bigot (1939) are also referable to *L. ferox*.

DESCRIPTION OF HOLOTYPE. Sauvage's description of the holotype tooth (1873 : 379) repeated by Andrews (1913 : 10–11) leaves little to be added. The longitudinal ridges of the crown are coarse and on the external surface are unevenly spaced, with wide smooth areas between them.

DESCRIPTION OF ASSOCIATED SKELETON FROM PETERBOROUGH. *Teeth.* Indistinguishable from the type described and figured by Sauvage (1873).

Mandible. There are 24 alveoli present in the left ramus, and there were also probably 24 in the right. There are six pairs of large caniniform teeth in the symphysis and the mandible is somewhat expanded to accommodate them. The seventh tooth is greatly reduced, and from about the eleventh tooth, the teeth gradually diminish in size.

Cervical vertebrae. Andrews (1913, text-fig. 2), figured a cervical vertebra of this skeleton, but it is given a detailed description here as it is important in the specific diagnosis of this form. The anterior articular surface is somewhat heart-shaped in outline, with the ventral margin produced to form a small " v " in the mid-line. The surface is concave with a deep pit at the centre, no mamilla being developed. The margins are gently bevelled and are sharply delimited by a continuous peripheral groove. The posterior articular surface is similar to the anterior but the margin is strongly bevelled in the ventral quadrant so that it appears to be folded over on to the ventral surface of the centrum. In ventral view the centrum is produced anteriorly in the mid-line to form a ventral lip which in anterior view is cut off by the peripheral groove. There is no ventral keel in the mid-line.

Scapula. The scapula (Pl. 24, fig. 3) is poorly preserved, but it shows the kind possessed by the genus *Liopleurodon*. The short stout glenoid ramus bears an articular facet for the coracoid, and in ventral view a ridge can be observed extending from the glenoid cavity anteriorly. The narrow dorsal process which is directed postero-laterally is set off from the plane of the rest of the bone by this ridge.

Propodials. The femur is figured (Pl. 24, fig. 4) for the first time. It is of special interest as it has almost parallel sides for the greater part of its length. Its distal articular surface also shows a well-marked facet for a pisiform bone in addition to the normal articular facets. This is worthy of mention as it has generally been believed that such pisiform bones were not present until Cretaceous times.

Epipodials. The tibia and fibula are considerably longer than wide.

Liopleurodon pachydeirus (Seeley)

(Pl. 25 ; Pl. 28, figs. 1–1*b*)

1869. *Pliosaurus pachydeirus* Seeley, p. 118.
1888. *Pliosaurus ferox* (Sauvage) : Lydekker, p. 353.
1889*b*. *Pliosaurus ferox* (Sauvage) : Lydekker, pp. 145–147.
1890. *Pliosaurus ferox* (Sauvage) : Lydekker, pp. 49–52, pl. 5.
1905. *Liopleurodon ferox* Sauvage : Blake, pp. 23–25, pl. 1, figs. 1, 2.
1913. *Pliosaurus ferox* (Sauvage) : Linder, pp. 375–390, text-figs. 24–32 ; pl. 35, figs. 3–8.
1913. *Pliosaurus ferox* (Sauvage) : Andrews, pp. 23–24, text-figs. 4, 6A.
1949. *Pliosaurus* cf. *ferox* (Sauvage) : Follet, pp. 22–24, text-fig. 1.
1958. *Pliosaurus pachydeirus* Seeley : Tarlo, pp. 440–441.

DIAGNOSIS. Teeth with fine closely packed enamel ridges on inner surface and 6–8 evenly spaced ridges on outer surface. Cervical vertebrae with length about half width or height, with faint ventral keel.

MATERIAL. Holotype, a series of associated cervical vertebrae (J.46912), Sedgwick Museum, Cambridge, from Oxford Clay of Great Gransden. Associated skeleton R.2446, British Museum (Nat. Hist.), described and figured Lydekker (1890).

HISTORY OF THE SPECIES. Seeley (1869 : 118) listed an atlas and axis together with fifteen cervical vertebrae from the Oxford Clay of Great Gransden, which he named *Pliosaurus pachydeirus*, but since he gave no description of them the name was invalid. These vertebrae were included in the species *P. ferox* by Lydekker (1888, 1889*b*). Lydekker (1890) described and figured an Oxfordian pliosaur skeleton under the name *Pliosaurus ferox* (Sauvage) as its cervical vertebrae resembled the " associated series to which Professor Seeley applied the name of *Pliosaurus pachydeirus* ", but he recognized that its teeth differed from the type of *L. ferox* in that the " intercarinal space " was " scarcely definable " and the longitudinal ridges of the enamel were rather more " continuous and closer together ". Blake (1905) described similar teeth under the name *Liopleurodon ferox*, recognizing that they were similar to those described by Lydekker (1890). In 1913 Andrews correctly described as *P. ferox* part of an Oxfordian pliosaur skeleton which had teeth indistinguishable from Sauvage's type tooth, but with cervical vertebrae quite different from those figured by Lydekker (1890) as *P. ferox*. These two skeletons, which are re-described here, are obviously closely related, but as they differ in the characters of their teeth and cervical vertebrae I consider them to be specifically distinct, and am assigning the material described by Lydekker (1890) to Seeley's species which thus becomes *Liopleurodon pachydeirus* (Seeley). The skeleton described as *Pliosaurus ferox* by Linder (1913) is referable to *L. pachydeirus* on the characters of its cervical vertebrae.

DESCRIPTION OF HOLOTYPE. The cervical vertebrae listed by Seeley (1869) are described and figured here for the first time. These cervical vertebrae are similar to those of *L. ferox*, but can be distinguished from them as they are proportionately greater in length, possess a faint ventral keel, but have no ventral lip. The measurements in mm. of some of the type centra are given in the following table :

Cervical centra		Length	Width	Height
J.46912	1	45	96	87
,,	2	46	97	88
,,	3	47	99	88
,,	4	48	104	93
,,	5	49	109	97
,,	6	50	115	102

DESCRIPTION OF ASSOCIATED SKELETONS FROM PETERBOROUGH. *Teeth.* These are all circular in cross-section. The longitudinal ridges on the enamel of the crown are finer and more closely packed on the internal surface than in *L. ferox*. On the outer convex surface there are approximately 6–8 evenly spaced ridges. In this latter feature these teeth contrast markedly with those of *L. ferox*.

Mandible. According to Lydekker (1890 : 50) the mandibular symphysis extends back to the seventh tooth, but the only part of the mandible now known is that figured in Pl. 6, fig. 3 which bears 3–4 pairs of large caniniform teeth posterior to which the symphysis ends. All the teeth in the symphysis were large and caniniform and no series of smaller teeth was included in it as in *P. brachydeirus*. Thus in this feature *L. pachydeirus* is indistinguishable from *L. ferox*, and can be included in the same genus—*Liopleurodon*.

Cervical vertebrae. The cervical vertebrae described by Lydekker (1890) accord well with the type and are easily distinguished from *L. ferox* by their comparatively greater length and faint ventral keel.

Propodials. The femur is known and was figured, together with the tibia and fibula, by Andrews (1913) as *P. ferox*. If the femora of *L. pachydeirus* and *L. ferox* are compared, it can be seen that their proportions are very different. Although generally one cannot differentiate species on propodials, in this case it appears possible.

Epipodials. The tibia and fibula are longer than they are wide, as in other Oxfordian pliosaur species.

Genus *PELONEUSTES* Lydekker, 1889

Emended diagnosis. Mandible with very long symphysis bearing 13–14 pairs of teeth, of which the anterior 6–7 are large and caniniform ; total of about 40 teeth in each ramus. Teeth circular in section ; the majority of longitudinal enamel ridges reach half-way up the crown, relatively few continuing to the tip. Cervical vertebrae short, length slightly more than half the width or height ; well-marked ventral keel. Scapula triradiate with dorsal process directed laterally and ventral plate expanded medially. Epipodials long.

Type species : *Peloneustes philarchus* (Seeley).

Peloneustes philarchus (Seeley)

(Pl. 26 ; Text-fig. 9)

1869. *Plesiosaurus philarchus* Seeley, pp. 139–140.
1869. *Pliosaurus evansi* Seeley, pp. 116–117.
1877. *Pliosaurus evansi* Seeley : Seeley, pp. 716–723, text-figs. 1–9.
1888. *Thaumatosaurus philarchus* (Seeley) Lydekker, pp. 352–353.
1889. *Peloneustes philarchus* (Seeley) Lydekker, pp. 49–50, text-fig. 1A.
1889*a*. *Peloneustes philarchus* (Seeley) : Lydekker, pp. 48–56, text-figs. 4–9, pl. 2.
1889*b*. *Peloneustes philarchus* (Seeley) : Lydekker, pp. 151–152, 154–158, text-figs. 47A, 48, 49, 51–55.
1892. *Pliosaurus philarchus* (Seeley) Seeley, p. 127.
1908. *Peloneustes philarchus* (Seeley) : Jaccard, pp. 395–398, pls. 26–32.
1913. *Peloneustes philarchus* (Seeley) : Linder, pp. 341–367, 369–375 ; text-figs. 1–21 ; pls. 33, 34, 35, figs. 1, 2.
1913. *Peloneustes philarchus* var. *spatyrhynchus* Linder, pp. 368–369, text-figs. 22–23.
1913. *Peloneustes philarchus* (Seeley) : Andrews, pp. 34–70, 202, text-figs. 11–26, 27A ; pl. 4.

Diagnosis. As for genus (only species).

Material. Holotype, J.46913, Sedgwick Museum, Cambridge, associated skeleton from Oxford Clay of Peterborough.

History of the species. Seeley (1869 : 139–140) gave a brief description of an associated pliosaur skeleton from the Oxford Clay of Peterborough which he named *Plesiosaurus philarchus*. In 1888 Lydekker transferred the species to Meyer's genus *Thaumatosaurus*. Lydekker (1889*a*) described further material of the same species and proposed the new generic name *Peloneustes*. Later, (1889*b*) he figured a cervical centrum and, in his diagnosis of the genus *Peloneustes* he claimed that the cervical centra were " without a haemal ridge " (ventral keel), although his figure gives no evidence either way. This last point is of some importance, since in fact the cervical vertebrae of *Peloneustes philarchus* have a well-marked ventral keel and are distinguished from those of *Pliosaurus andrewsi* by its presence.

Seeley (1892) claimed that the species *P. philarchus* could not be generically separated from *Pliosaurus*, but though it is evident that it is somewhat like *Pliosaurus brachydeirus* in the character of the mandibular symphysis, since the name *Peloneustes* has become so well established in the literature it is not proposed to revise it. Jaccard (1908), Andrews (1913) and Linder (1913) described complete skeletons of *Peloneustes philarchus*, and Linder erected the new subspecies *Peloneustes philarchus* var. *spatyrhynchus* for a form in which the anterior part of the mandibular

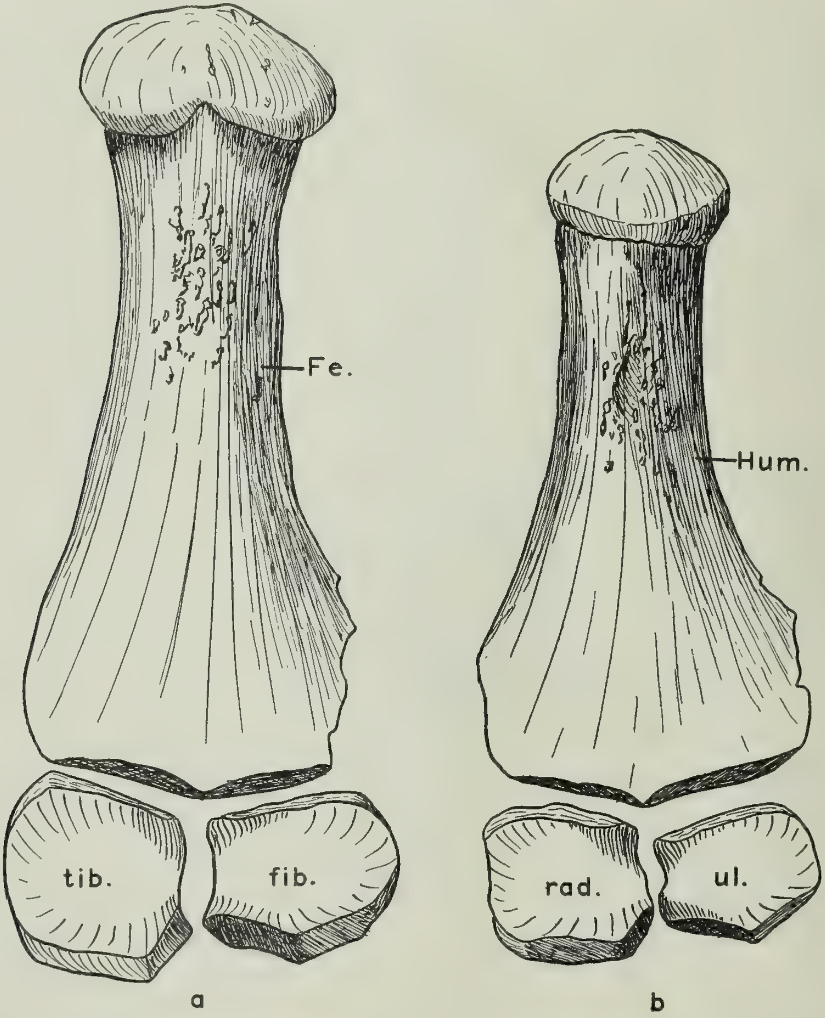


FIG. 9. *Peloneustes philarchus* (Seeley), holotype. J.46913, Sedgwick Mus. Propodials and epipodials in ventral view, × ¼. *a*. right hind limb; *b*. right forelimb. HUM., humerus; FE., femur; fib., fibula; rad., radius; tib., tibia; ul., ulna.

symphysis was spatulate. The osteology of *Peloneustes philarchus* is known in detail, but the holotype itself has never been adequately described or figured. Since it is important to have a published record of the holotype, the skeleton originally listed by Seeley as *P. philarchus* is here figured and described for the first time.

DESCRIPTION OF HOLOTYPE. *Teeth.* A number of teeth are known from the type skeleton, but apart from one fragment (Pl. 26, fig. 3) all have the distal part of the crown missing. The fragment which is reasonably complete shows that most of the fine longitudinal ridges reach half-way up the crown, a few ridges only continuing to the tip. This character is extremely distinctive and serves to separate this species from the other known Oxfordian species. Andrews (1913 : 202) described such teeth in his description of material assigned to *Peloneustes philarchus.*

Mandible. The mandible measures 740 mm. in length. There are 38 alveoli preserved in the right ramus, but the immediate post-symphysial portion of the left ramus is missing. Thirteen to fourteen pairs of teeth are included in the symphysis of which the anterior 6–7 pairs are large and caniniform. This species has a comparatively longer mandibular symphysis than any other pliosaur and is generically separated from *Pliosaurus* on this account.

Cervical vertebrae. The articular surfaces of the cervical vertebrae are strongly concave with markedly bevelled margins. In several of the more anterior centra a pronounced ventral lip is developed, to which Lydekker (1889*b*) drew attention. In ventral view there is a distinct ventral keel in the mid-line. The cervical centra of *Pliosaurus evansi* are indistinguishable from these.

Pectoral girdle. The pectoral girdle is better known from specimens in the British Museum (Nat. Hist.) in which there is a triangular interclavicle in addition to the scapula and coracoids. Only the glenoid portions of the scapulae are preserved in the holotype, but I have figured a scapula here showing the typical form of the pliosaur scapulae with the dorsal process produced laterally and a ridge on the ventral surface extending towards the anterior part of the ventral plate.

Propodials and epipodials. All four limbs are preserved together with their epipodials and tarsal and carpal elements. A humerus and femur are figured together with their epipodials (Text-fig. 9). The epipodials are of considerable interest since the tibia and radius are greater in length than in width, whilst in the fibula and ulna the reverse is the case. Were these bones found isolated, the radii and tibiae would be considered Oxfordian in age, and the fibulae and ulnae Kimeridgian. Obviously there was considerable variation in this part of the skeleton since in other skeletons of this species all the epipodials are longer than they are broad.

Genus ***SIMOLESTES*** Andrews, 1909

EMENDED DIAGNOSIS. Mandible with very short spatulate symphysis bearing 5–6 pairs of large caniniform teeth ; total of approximately 25 teeth in each ramus. Scapula triradiate, dorsal process directed laterally. Epipodials long.

TYPE SPECIES : *Simolestes vorax* Andrews.

Simolestes vorax Andrews

(Pl. 27 ; Pl. 28, figs. 3–3*b*)

1909. *Simolestes vorax* Andrews, pp. 423–429, text-figs. 4–7.
1911. *Thaumatosaurus calloviensis* Bogolubov, pp. 200–203, pl. 2, figs. 1, 6.
1913. *Simolestes vorax* Andrews : Andrews, pp. 25–34, pl. 3, text-figs. 8–10.

EMENDED DIAGNOSIS. Teeth circular in section ; few longitudinal enamel ridges on outer surface (absent altogether in largest teeth), beginning part-way up the crown leaving a smooth area at the base of the outer surface. Cervical vertebrae short, length about half width or height, ventral keel absent.

MATERIAL. Holotype, R.3319, British Museum (Nat. Hist.), complete associated skeleton, Oxford Clay, Peterborough.

HISTORY OF THE SPECIES. Andrews (1909) erected this species and the new genus *Simolestes* on a complete skeleton of which he gave a careful description. Later (1913) he re-described and figured the type skeleton more fully. The original generic and specific descriptions have required no further revision. Discussion has tended to centre around the family position of the species. It was recognized by Andrews to be a fairly typical pliosaur. White (1940), however, placed it in the family Elasmosauridae—thus associating it with the most advanced forms of the long-necked plesiosaurians, but this is incorrect. Recently Romer (1956) also excluded *Simolestes* from the pliosaurs including it in a new family, the Thaumatosauridae based on the genus *Thaumatosaurus* which is shown below to be invalid. *Simolestes vorax* is certainly a pliosaur and an immature skeleton of the same species is described below, together with part of the holotype.

DESCRIPTION OF HOLOTYPE AND SKELETON OF IMMATURE INDIVIDUAL. *Teeth.* These are all circular in section and are ornamented by fine longitudinal ridges on the enamel : the ridges are more numerous on the inner surface of the crown and those on the outer surface always begin some distance from the base, so that there is a roughly semicircular area at the base of the outer surface of the crown which is devoid of ornament. This is a constant feature of the teeth of this species and can be used in its recognition. It should, however, be noted that in the very largest teeth there is often no ornamentation at all on the outer surface of the crown, and the teeth are then hardly distinguishable from those of *Pliosaurus andrewsi*.

Mandible. In the holotype, the snout of the animal is preserved with the mouth closed, so that it is not possible to see the mandible in dorsal view. The smaller individual (R.3170) has the mandible isolated and the symphysial portion is excellently preserved (Pl. 27, fig. 4). The symphysis is extremely short and so expanded that its 5 pairs of large caniniform teeth are set almost in a circle. I find it difficult to offer any functional explanation of this remarkable dentition.

Cervical vertebrae. The vertebral column of the holotype is preserved in natural articulation but the detailed characters of its cervical vertebrae have not previously been recorded. The cervical vertebrae of the immature specimen are so badly preserved as to be hardly recognizable. There is no ventral keel on the ventral surface ; on the anterior margin a ventral lip is produced anteriorly, but this only occurs in the first few cervical centra. The articular surfaces are concave with a marginal bevel limited peripherally by a narrow groove. In lateral view, a faint ridge is developed extending from the apex of the triangular superior rib facet to the base of the neural arch.

Scapulae. The scapulae differ significantly from those of the other Oxfordian pliosaur species. The dorsal process is long and fairly narrow, directed posterolaterally, and set off from the plane of the rest of the bone. The ventral plate also forms a narrow process, about the same width as the dorsal process. It is not expanded to any degree and thus contrasts strongly with the scapula of *Peloneustes philarchus* and other Oxfordian pliosaurs.

Propodials. A humerus of the immature individual (Pl. 27, fig. 6) shows that the propodials differ from the holotype in that they do not possess the marked tuberosity midway down the posterior edge of their shafts. This feature was considered to be of diagnostic value by Tarlo (1958), but this view is erroneous. The propodials of *Simolestes vorax* are similar to those of most other pliosaurs and are valueless for the recognition of species.

Simolestes nowackianus Huene

1938. *Simolestes nowackianus* von Huene, pp. 370–376, text-figs. 1, 2.

EMENDED DIAGNOSIS. Teeth circular in section ; ornamentation of fine closely packed longitudinal striations. Cervical vertebrae not known.

MATERIAL. Holotype, symphysial portion of mandible, Tubingen University Museum, Oxfordian, Abessinien.

HISTORY OF THE SPECIES. von Huene (1938) described a mandible similar to that of *S. vorax.* He suggested that the specimen represented a new species of *Simolestes* as the teeth were ornamented differently from those of *S. vorax.* Although no other parts of the skeleton are known von Huene's species *Simolestes nowackianus* may be accepted as a valid species.

III. SPECIES TEMPORARILY RETAINED

GAMMA. *Pleiosaurus gamma* Phillips

Type. Anterior cervical centrum from the Oxford Clay of Weymouth figured Phillips (1871, fig. 152).

Phillips (1871) erected this name to include a number of cervical, dorsal and caudal vertebrae from the Kimeridge Clay of Shotover and the Oxford Clay of Weymouth. Only the cervical vertebrae are sufficiently distinctive to be of any taxonomic value and the Weymouth centrum, J.10455 in the University Museum, Oxford, is here selected as the lectotype. The name *Pliosaurus gamma* Phillips is retained only for the two cervical centra from the Oxford Clay of Weymouth.

GROSSOUVREI. *Liopleurodon grossouvrei* Sauvage

Holotype. Tooth from Kellaways Rock, figured Sauvage (1873, pl. 7, fig. 2).

Lydekker (1889*b*) described several teeth from the Coral Rag of Heddington Wiltshire (one of which he figured) under the name *Pliosaurus grossouvrei* and commented that they were very probably identical with those of *Pliosaurus evansi* (= *P. andrewsi*). These teeth are assigned to *Pliosaurus andrewsi* and the name *L. grossouvrei* is retained for the holotype and all similar teeth from the Kellaways Rock.

IRGISENSIS. *Peloneustes irgisensis* Novozhilov

Holotype. Skull described and figured Novozhilov (1948 : 118, fig. 1*b*).

This species is based on a skull which differs from that of *Peloneustes philarchus* in several respects. These differences may well be due to the fact that Novozhilov was describing a skull of *Pliosaurus* under the impression gained from the literature, that only *Peloneustes* was long-snouted. Until further description of Novozhilov's specimen is forthcoming I prefer to place his species in the genus *Pliosaurus*. At the moment I am unable either to accept or reject the validity of his specific name.

ROSSICUS. *Pliosaurus rossicus* Novozhilov

Holotype. Skull described and figured Novozhilov (1948 : 115, fig. 1*a*).

Novozhilov described a pliosaur skeleton from the Lower Volgian to which he gave the new specific name *P. rossicus*. The main features of this specimen are that the teeth are trihedral in cross-section, thus confirming its Kimeridgian age ; the scapula, according to Novozhilov, is like that of *Kronosaurus* (i.e., like that of *Pliosaurus* L.B.T.), thus confirming the inclusion of the species in *Pliosaurus*. Only the skull is figured and there is no description of the mandibular symphysis. Furthermore there is no indication of the characters of the cervical vertebrae. Until more is known I hesitate to accept Novozhilov's species as valid.

IV. INVALID SPECIES

AEQUALIS. *Pleiosaurus aequalis* Phillips

Holotype. Femur from Kimeridge Clay of Swindon, figured Phillips (1871, fig. 164).

Lydekker (1889*b*) placed this species in the genus *Peloneustes*, thus extending the range of the genus into the Kimeridgian. Since I have found propodials to be of little taxonomic value, this species (based on an isolated limb bone) is here considered invalid, retaining *Peloneustes* as an Oxfordian form only. (*Peloneustes kanzleri* Koken is a Cretaceous Elasmosaur.)

ARCHIACI. *Polyptychodon archiaci* Deslongchamps

Type. Mandible from Kimeridge Clay of Le Havre, figured Deslongchamps (?1872, pl. 5, figs. 1, 2).

The same specimen was figured by P. Fischer (1869) under the name *Pliosaurus grandis* (Owen). The mandible figured by P. Fischer and by Deslongchamps has a short mandibular symphysis bearing 6 pairs of large caniniform teeth, and on this basis can be provisionally included in the Kimeridgian species *Stretosaurus macromerus* (Phillips).

CALLOVIENSIS. *Thaumatosaurus calloviensis* Bogolubov

Holotype. Tooth from the Callovian of Moscow, figured Bogolubov (1912, pl. 2, figs. 1, 6).

This tooth bears fine longitudinal enamel ridges which begin part-way up the crown on the external surface—a feature characteristic of *Simolestes vorax* Andrews. Consequently *T. calloviensis* is included in the synonymy of *S. vorax*.

EVANSI. *Pliosaurus evansi* Seeley

Holotype. Associated cervical vertebrae from the Oxford Clay of St. Neots, Cambridgeshire, described Seeley (1869).

Seeley (1877) described and figured part of the type skeleton noting the presence of a marked ventral keel on the centra. Lydekker (1890) referred the species to the genus *Peloneustes*, and later (1890*a*) recognized that the cervical vertebrae of *Peloneustes evansi* "can only be distinguished by their larger dimensions" from *P. philarchus* (Seeley).

Since the cervical vertebrae are the only parts of the skeleton by which the type specimens of *P. evansi* and *P. philarchus* can be compared, it appears that a single species is represented. In view of this, *P. evansi* is taken to be a subjective synonym of *Peloneustes philarchus*.

Lydekker (1890*a*) referred the large mandible figured by Phillips (1871) as *Pleiosaurus ?grandis*, to *Peloneustes evansi*. Andrews (1913) described under the name *Peloneustes evansi* an associated skeleton with a mandible similar to that figured by Phillips (1871). He noted that there were 11–12 pairs of teeth in the mandibular symphysis. In this feature, the mandible agrees closely with that of *Pliosaurus brachydeirus* Owen, the type species, and should therefore have been put in the genus *Pliosaurus*. The cervical vertebrae of the associated skeleton described by Andrews are dissimilar to those of Seeley's type of *Pliosaurus evansi*; they should therefore not have been given the name of *evansi*. The skeleton described by Andrews has consequently been made the holotype of a new species—*Pliosaurus andrewsi* (see p. 163).

FREARSI. *Spondylosaurus frearsi* Fischer de Waldheim

Holotype. Anterior cervical centrum from the Kimeridge Clay of the Moscow Basin, figured Fischer de Waldheim (1845, pls. 7, 8).

The material collected by Mr. Frears " an intelligent English gentleman resident in Moscow ", and described by Fischer de Waldheim, was at the same time identified by Owen (1845) as *Plesiosaurus brachyspondylus.* Lydekker (1889*b*), however, considered Fischer's species to be a synonym of the Oxfordian *Pliosaurus grossouvrei* (Sauvage). From a comparison of Fischer's original figures and the specimens of *Pliosaurus brachyspondylus* (Owen) described by Tarlo (1959), *Spondylosaurus frearsi* can be considered a synonym of Owen's species.

GIGANTEUS. *Plesiosaurus giganteus* Conybeare

The name *Plesiosaurus giganteus* was erected by Conybeare (1824*a*) to include all Plesiosaurians with shortened cervical vertebrae, and no types were designated and no descriptions given. The cervical vertebrae from the Kimeridge Clay of Weymouth, figured by Conybeare (1824) and the associated skeleton from the Kimeridge Clay of Market Rasen were included in this species, which has generally been considered invalid as it was insufficiently characterized.

GIGANTEUS. *Pliosaurus giganteus* Wagner

Holotype. Tooth described and figured Wagner (1852, pl. 20). This tooth has a pattern of longitudinal enamel ridges on its crown similar to *Liopleurodon ferox* Sauvage. The cross-section of the tooth is also circular, confirming its Oxfordian age. Lydekker (1889*b*) placed *P. giganteus* Wagner in the synonymy of the Kimeridgian *P. macromerus* Phillips, since the specific name had already been employed for pliosaur remains by Conybeare (1824*a*). Wagner's specimen differs from all Kimeridgian pliosaur teeth in having a circular cross-section to its crown and it is here considered conspecific with the Oxfordian species *Liopleurodon ferox* Sauvage.

GIGANTEUS. *Pliosaurus giganteus* Trautschold

Holotype. A tooth from the Oxfordian of the Moscow Basin, described and figured by Trautschold (1860, pl. 8, fig. 25).

This tooth is referred to *Liopleurodon ferox* Sauvage, Trautschold's trivial name being pre-occupied by Wagner (1852) and by Conybeare (1824*a*).

GRANDIS. *Plesiosaurus grandis* Owen

Syntypes. Three isolated propodials and a triradiate scapula, all of which can no longer be traced. Unfortunately none of this material was ever adequately described or figured. Owen (1841*a*) transferred the species to *Pliosaurus*, and later (1861, 1863) he considered *Pliosauris grandis* to be the type species. However, as Lydekker (1889*b*) pointed out, there was no evidence that the types of *P. grandis* even belonged to pliosaurs. Clearly this species is invalid, being based on indeterminate material.

Unfortunately Owen (1869*a*) described and figured a large pliosaur mandible from the Kimeridge Clay under the name *Pliosaurus grandis.* This mandible has 6 pairs of large caniniform teeth in its symphysis, a character until now considered typical of *Pliosaurus*, although the type species *P. brachydeirus* has 10–12 pairs of teeth in the mandibular symphysis. Lydekker (1889*b*) placed the large mandible described by Owen in *Pliosaurus macromerus* Phillips to which species the mandible described by P. Fischer (1869) as *P. grandis* and by Deslongchamps (?1872) as *Polyptychodon archiaci*, is assigned.

The name *P. grandis* has most regrettably persisted and it is to be found in such recent works as White (1940), Welles (1943) and Piveteau (1955). It is an invalid specific name and material similar to that described by Owen in 1869 can be tentatively assigned to *Stretosaurus macromerus* (Phillips).

MERIANI. *Ischyrodon meriani* von Meyer

Holotype. Tooth from Oxfordian of Argau Canton, Switzerland, described and figured von Meyer (1856*a*, pl. 2, figs. 1–3).

The name was erected in 1838 by von Meyer but remained a *nomen nudum* until 1856. Meyer (1856*a*) considered the tooth to be of Bradfordian age but the associated invertebrate fossils suggest Oxfordian. Lydekker (1889*b*) provisionally referred Meyer's material to the Kimeridgian species *P. macromerus* on the basis of its size. The circular cross-section of the crown of *Ischyrodon meriani* indicates Oxfordian age rather than Kimeridgian, since all known Kimeridgian pliosaurs possess teeth with a characteristic trihedral section. The tooth figured by Meyer is here provisionally included in *Liopleurodon ferox* since it clearly does not belong to any of the other five well-known Oxfordian species.

MOSQUENSIS. *Thaumatosaurus mosquensis* Kiprijanoff

Type. Anterior cervical vertebra from Oxfordian of Moscow Basin figured Kiprijanoff (1883, pl. 14, fig. 1), here selected as lectotype.

Lydekker (1889*b*) included this species in the synonymy of *P. ferox.* If Kiprijanoff's figures are compared with the associated cervical vertebrae of *L. ferox* figured by Andrews (1913) it is evident that they are conspecific, thus *T. mosquensis* is here considered a subjective synonym of *L. ferox.*

NITIDUS. *Pleiosaurus nitidus* Phillips

Type. Posterior cervical centrum from Kimeridge Clay of Shotover, figured Phillips (1871, fig. 156).

Lydekker (1889*b*) considered this species to be an immature form, but he noted that it closely accorded with the posterior cervical centrum of *Pliosaurus brachyspondylus* (since erected as the neotype). Phillips' sketch seems to be very similar to *P. brachyspondylus*, so I take *P. nitidus* to be a synonym of *Pliosaurus brachyspondylus* (Owen).

OOLITHICUS. *Thaumatosaurus oolithicus* Meyer

Syntypes. Miscellaneous fragments of teeth, jaws, ribs and vertebrae from the ? Oxfordian of Württemberg. These remains were described by von Meyer in 1841 but were not figured until 1856. The fragments figured are pliosaurian but are quite indeterminable, and both specific and generic names must be rejected.

NOTE ON THE GENUS *Thaumatosaurus.*

The genus *Thaumatosaurus* was proposed by von Meyer (1841) to cover a collection of indeterminate pliosaur fragments from the lower part of the Upper Jurassic (or the top of the Middle Jurassic). Lydekker (1889*b*) accepted the validity of this genus and included within it a number of Plesiosaur species including the Liassic *Plesiosaurus cramptoni* Carte & Bailey, for which Seeley (1874) had earlier proposed the generic name *Rhomaleosaurus.* In 1910 Fraas described a complete skeleton of a Liassic plesiosaur under the name of *Thaumatosaurus victor.* This specimen is so beautifully preserved that it has found its way into most text-books of vertebrate palaeontology. Although *T. victor* is preserved in ventral view and *Rhomaleosaurus cramptoni* in dorsal, there is no doubt that they belong to the same genus. As Andrews (1922) recognized, *Rhomaleosaurus* is a valid generic name for plesiosaurians with long necks and comparatively large heads. *T. victor* Fraas should therefore be named *Rhomaleosaurus victor* (Fraas).

It is important for the genus *Thaumatosaurus* to be rejected as its continued use in the literature leads to a great deal of confusion.

PLANUS. *Pliosaurus planus* Hulke

Holotype. Scapula from Kimeridge Clay of Shotover, noted Hulke (1883), figured Lydekker (1889*b*, fig. 36).

This scapula (which Hulke associated with a coracoid from the Oxford Clay) belongs to an immature *Pliosaurus.* It is specifically indeterminate but for the sake of convenience is described here under *P. brachydeirus.* The specific name used by Hulke was preoccupied by Owen (1864) for a Cretaceous elasmosaur.

PORTLANDICUS. *Pliosaurus portlandicus* Owen

Type. Right hind limb from the Portland Oolite of the Isle of Portland, figured Owen (1869, pl. 4). This limb, as shown by Seeley (1871) does not belong to a pliosaur but to a plesiosaur. Lydekker (1889*b*) placed it in the genus *Cimoliosaurus* ; Sauvage (1880) in *Muraenosaurus* ; and Bogolubov (1912) in *Colymbosaurus* : Savage (1958) erroneously retains the species in the genus *Pliosaurus* but Delair (1959) following Bogolubov correctly referred it to the plesiosaur genus *Colymbosaurus.*

RECENTIOR. *Plesiosaurus recentior* Parkinson

In 1822, Conybeare read a paper to the Geological Society of London in which he recorded for the first time the presence of plesiosaurians with shortened neck vertebrae in the Kimeridge Clay. These remains were not given a name and the paper which contained figures of pliosaur vertebrae from Weymouth, was not published until 1824. In the meantime, Parkinson (1822) published a book and gave the name *Plesiosaurus recentior* to plesiosaurians with shortened cervical vertebrae. Subsequently the name *P. recentior* was attributed to Conybeare by von Meyer (1832) and to von Meyer by Lydekker (1889*b*). The objections to Conybeare's specific name *giganteus* (p. 176) are equally applicable to Parkinson's *P. recentior*; no specific name can be used to include all plesiosaurians with shortened neck vertebrae.

SIMPLEX. *Pleiosaurus simplex* Phillips

Holotype. Propodial from Kimeridge Clay of Shotover, figured Phillips (1871, fig. 165).

Although this bone belongs to a pliosaur, it is specifically indeterminate.

STERRODEIRUS. *Plesiosaurus sterrodeirus* Seeley

Holotype. A basi-occipital and six vertebrae, all reputedly associated, from the Kimeridge Clay of Ely, described Seeley (1869).

These remains were placed in the species *Peloneustes aequalis* (Phillips) by Lydekker (1889*b*). I would tentatively assign them to *Pliosaurus brachydeirus* on the presence of a well-marked ventral keel on the cervical centra.

SUPRAJURENSIS. *Polycotylus suprajurensis* Sauvage

Holotype. Propodial bone from the Upper Kimeridge Clay, figured Sauvage (1876, pl. 1).

This supposed humerus belonged to a pliosaur but it is impossible to determine its specific identity.

SUPRAJURENSIS. *Pliosaurus suprajurensis* Sauvage

Holotype. Anterior cervical centrum from the Portlandian of Boulogne-sur-Mer, figured Sauvage (1879, pl. 27, fig. 1). This centrum is characterized by a prominent ventral keel and it can be assigned to *Pliosaurus brachydeirus* on this feature. It is included in the synonymy of the type species. The trivial name *suprajurensis* had already been used by Sauvage in 1876.

TROCHANTERIUS. *Plesiosaurus trochanterius* Owen

Syntypes. Propodials from Kimeridge Clay of Wiltshire, described Owen (1839).

These limb bones were transferred to *Pliosaurus* by Owen (1841*a*). However, these propodials belong to a plesiosaur and not to a pliosaur, as was recognized by

Sauvage (1876) who included the species in *Cryptocleidus*, and Bogolubov (1912) in *Colymbosaurus*. Delair (1959) follows Bogolubov in placing the species in *Colymbosaurus*. It is worth noting here that Owen (1869) described a large crocodilian mandible under the name *Pliosaurus trochanterius*.

WEIYUANENSIS. *Sinopliosaurus weiyuanensis* Young

Holotype. Tooth described and figured Young (1942, pl. 1, figs. 17–19).

Young (1942) described and figured a pliosaur tooth under the name *Sinopliosaurus weiyuanensis* Young. From the figures the specimen appears to be indeterminable and therefore in my opinion both the generic and specific names erected by Young are invalid.

Subsequently Young (1946) described further plesiosaurian remains as belonging to the same species including a tooth which, from his description, may well belong to *Pliosaurus andrewsi*.

WOSINSKII. *Pliosaurus wosinskii* Fischer de Waldheim

Holotype. Teeth in fragment of jaw from the Kimeridgian of the Moscow Basin, figured Fischer (1846, pls. 3, 4).

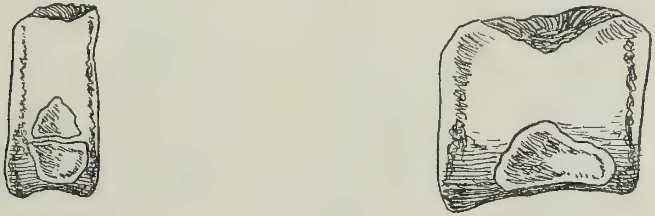
The crowns of these teeth have the typical trihedral cross-section common to all pliosaurs of Kimeridge age. The remains come from the same locality as *Spondylosaurus frearsi* (= *P. brachyspondylus*) and they may well belong to the same species. I have therefore tentatively included them in the synonymy of *Pliosaurus brachyspondylus* (Owen).

V. KEY TO THE IDENTIFICATION OF PLIOSAURS

1. Family Pliosauridae: Distinguishable on shortness of cervical vertebrae, proportions of propodials and elongated ischia.

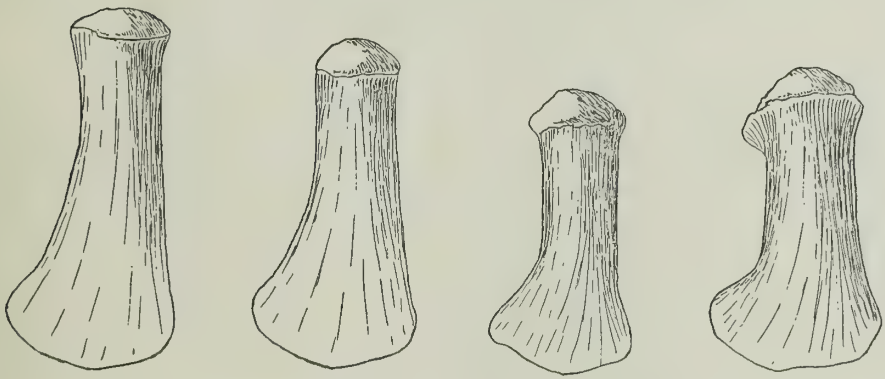
Pliosauridae

Elasmosauridae
(Upper Jurassic forms)



1a. 1b.

Cervical vertebrae in lateral view.



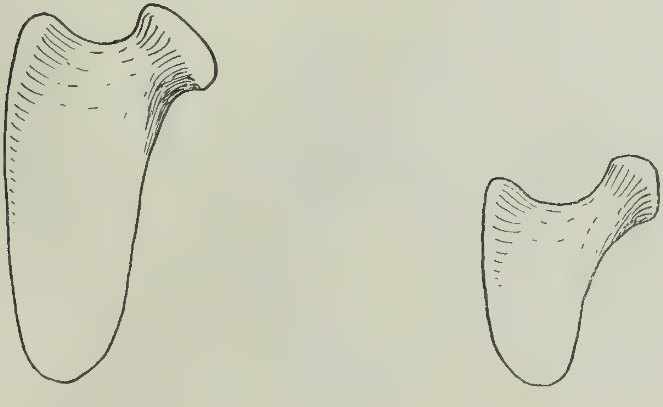
1c. femur

1d. humerus

1e. femur

1f. humerus

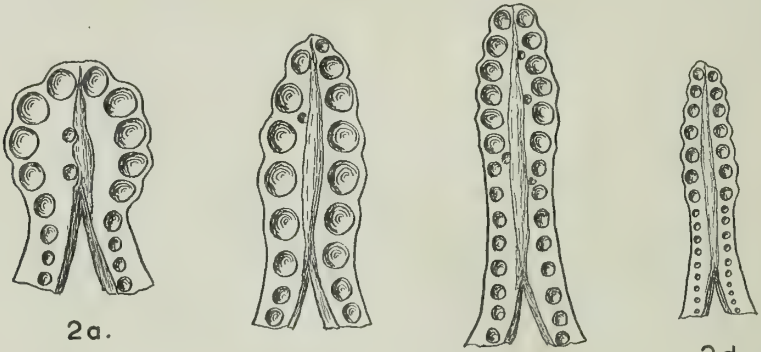
Propodials in dorsal view.



1g. 1h.

Ischia in dorsal view.

2. Genera : Pliosaur genera fall into four groups on the characters of the mandibular symphysis.



2a. *Simolestes*

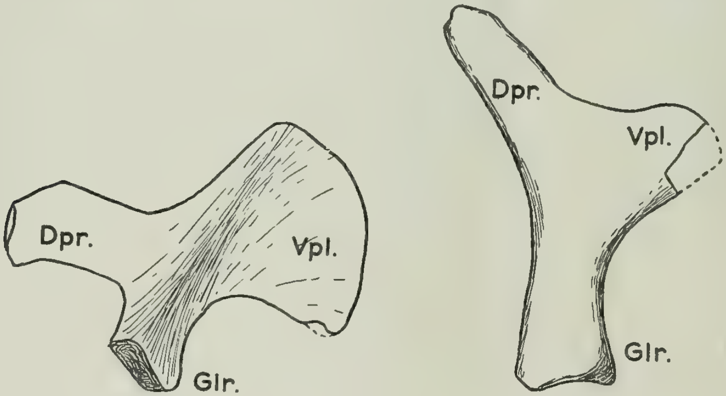
2b. *Liopleurodon-Stretosaurus*

2c. *Pliosaurus*

2d. *Peloneustes*

Mandibular symphyses in dorsal view.

The genera *Liopleurodon* and *Stretosaurus* can be distinguished on their scapulae.



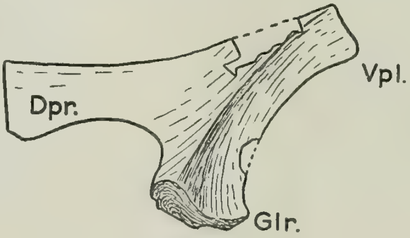
2e. *Liopleurodon*

2f. *Stretosaurus*

Scapulae in ventral view.

(Dpr., dorsal process ; Glr., glenoid ramus ; Vpl., ventral plate.)

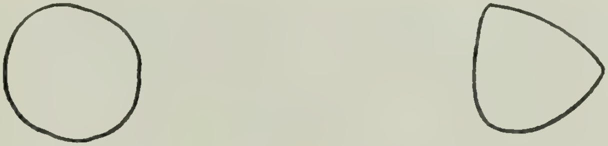
All pliosaur genera (with the exception of *Stretosaurus*) have scapulae of *Liopleurodon* type, although this pattern may be slightly modified, as in *Simolestes*.



2g. *Simolestes*

Scapula in ventral view.

3. Species: All pliosaurs can be separated into two groups on the cross-section of the crowns of their teeth. This is a horizontal division separating the Oxfordian species from those of Kimeridgian age.



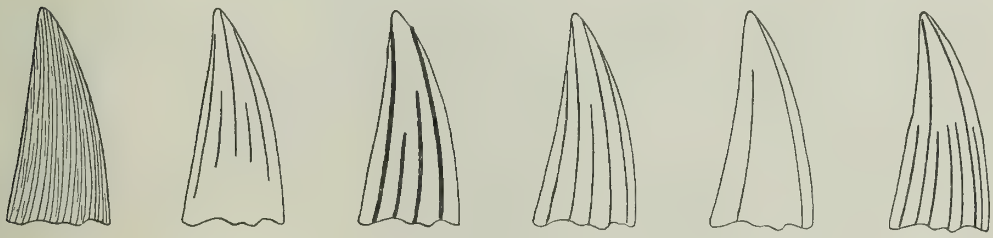
3a. *Oxfordian*

3b. *Kimeridgian*

Outline of teeth in cross-section.

The Kimeridgian species cannot be distinguished from one another by their teeth.

The Oxfordian species can readily be separated from one another on the ornamentation of the crowns of their teeth.



3c. *Simolestes nowackianus*

3d. *Simolestes vorax*

3e. *Liopleurodon ferox*

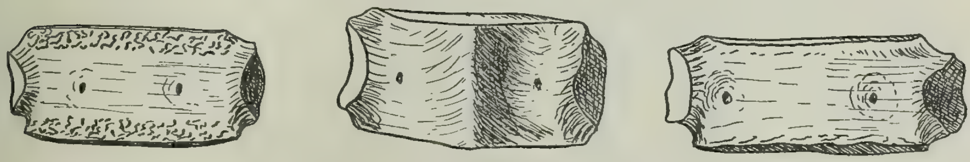
3f. *Liopleurodon pachydeirus*

3g. *Pliosaurus andrewsi*

3h. *Peloneustes philarchus*

Tooth crowns in external view.

The three Kimeridgian species can be separated on the character of their cervical vertebrae.



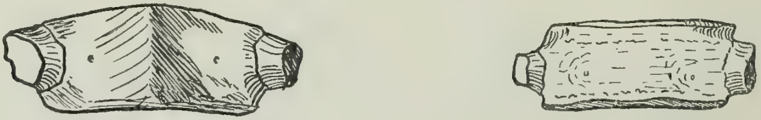
3j. *Pliosaurus brachyspondylus*

3k. *Pliosaurus brachydeirus*

3l. *Stretosaurus macromerus*

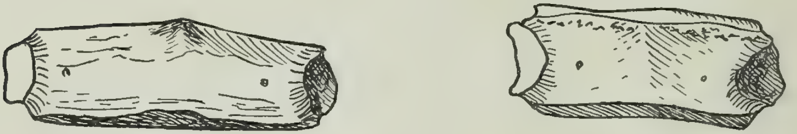
Cervical vertebrae in ventral view.

The specific distinctions of the Oxfordian pliosaurs can usually be supplemented by the characters of the cervical vertebrae.



3m. *Peloneustes philarchus*

3n. *Simolestes vorax-Pliosaurus andrewsi*



3p. *Liopleurodon ferox*

3q. *Liopleurodon pachydeirus*

Cervical vertebrae in ventral view.

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PLATE 20

Pliosaurus brachydeirus Owen, holotype, University Museum, Oxford.

FIG. 1. Mandible in dorsal view, J.9245B, × $\frac{1}{7}$.

FIGS. 2–2*b*. Anterior cervical centrum, J.9294, × 1; 2, anterior view, 2*a*, ventral view, 2*b*, lateral view of left side.

FIG. 3. Right femur in dorsal view, J. 9285, × $\frac{1}{5}$.

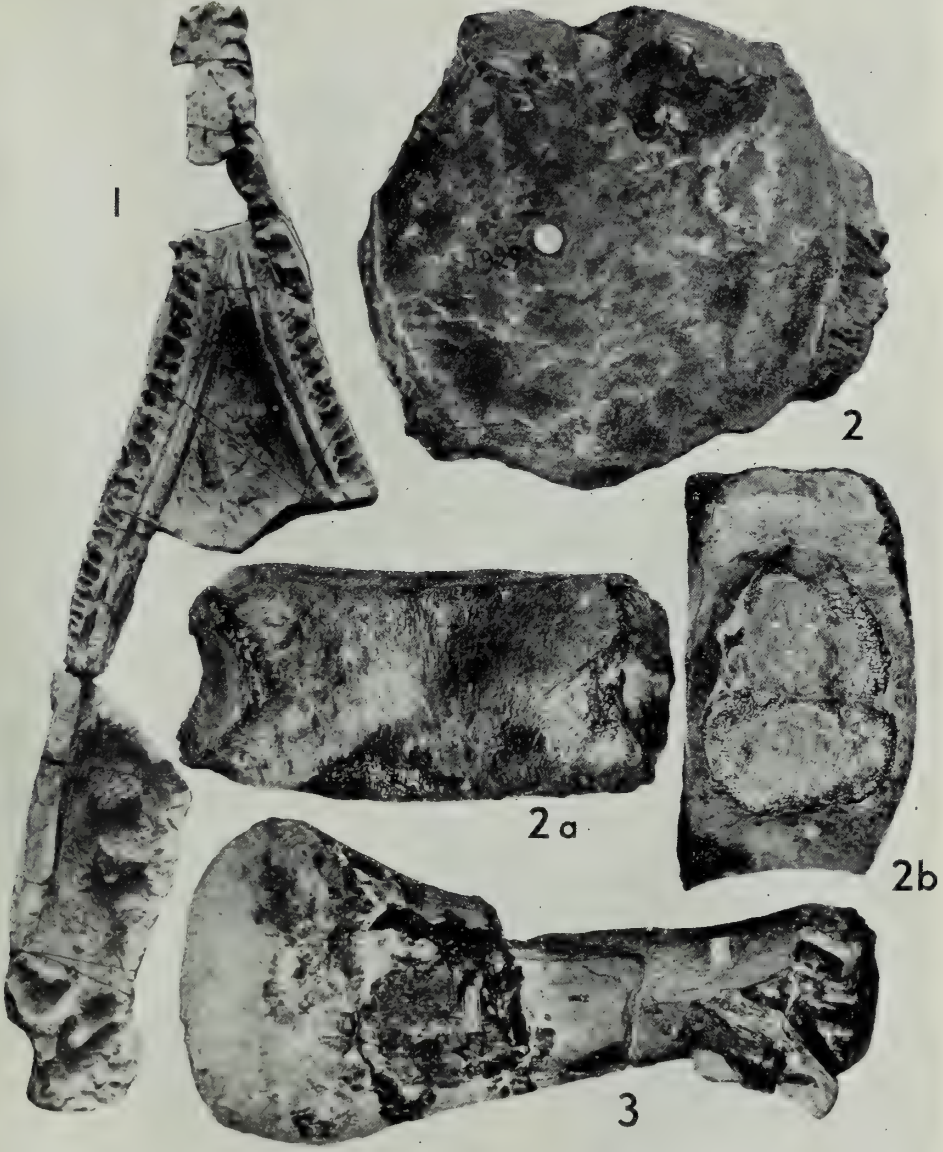
1
2
2a
2b
3

PLATE 21

Pliosaurus brachyspondylus (Owen), neotype, J.29564, Sedgwick Musuem, Cambridge.

FIGS. 1, 1*a*. Posterior cervical centrum, × 1; 1, anterior view, 1*a*, ventral view.

Associated skeleton, J. 35991, Sedgwick Museum, Cambridge.

FIG. 2. Mandible in dorsal view, × $\frac{1}{8}$.

FIGS. 3, 3*a*. Tooth × 1; 3 external view, 3*a*, lateral view.

FIG. 4. Left femur in dorsal view, × $\frac{1}{8}$.

Pliosaurus sp. FIG. 5. Right scapula R.287, Brit. Mus. (Nat. Hist.), in ventral view, × $\frac{1}{8}$.

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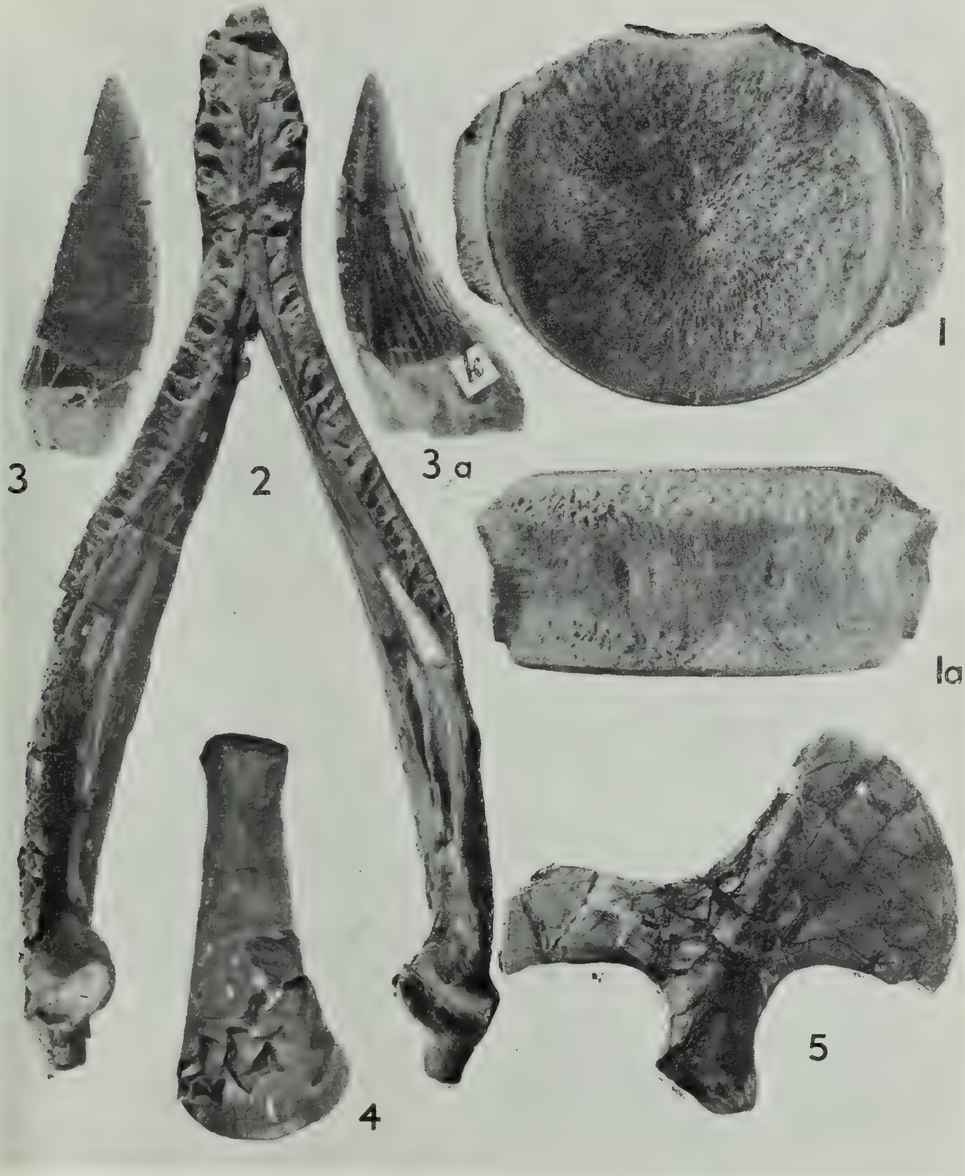
3
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3 a
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1a
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5

PLATE 22

Stretosaurus macromerus (Phillips), lectotype, J.10441, University Museum, Oxford.

FIGS. 1, 1*a*. Anterior cervical centrum, × $\frac{1}{3}$. 1, anterior view, 1*a*, ventral view.

Associated skeleton, J.35990, Sedgwick Museum, Cambridge.

FIG. 2. Left scapula in ventral view, × $\frac{1}{5}$.

FIG. 3. Anterior cervical centrum with cervical rib, in ventral view, × $\frac{1}{3}$.

FIG. 4. Anterior cervical centrum, in posterior view, × $\frac{1}{3}$.

Mandible J.10454, University Museum, Oxford.

FIG. 5. Dorsal view of symphysis, × $\frac{1}{7}$.

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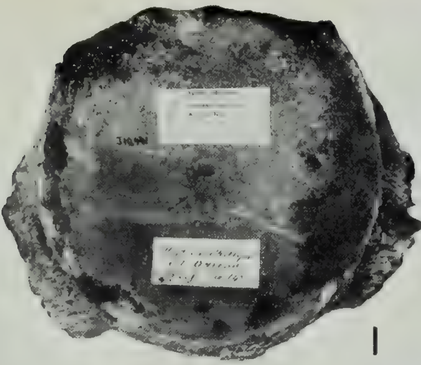
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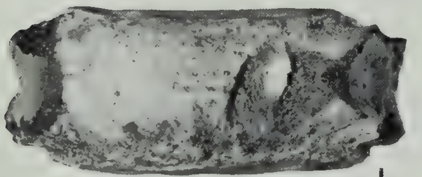
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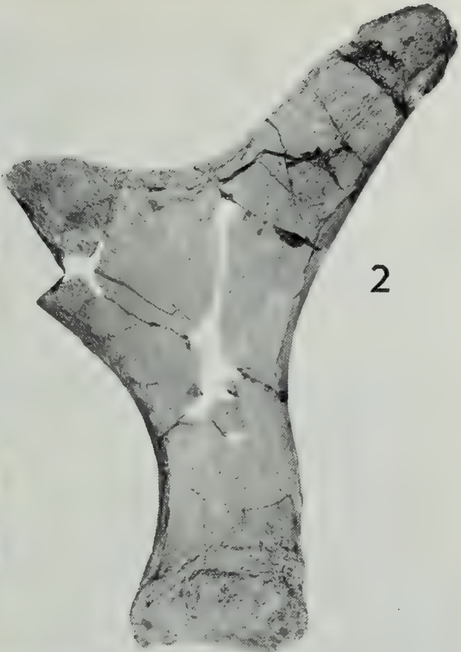
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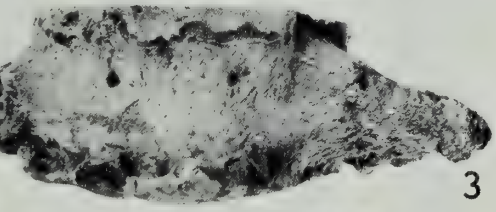
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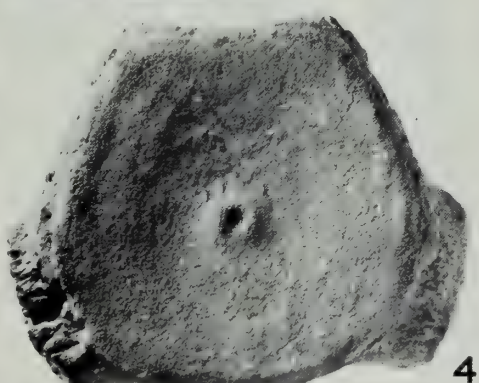
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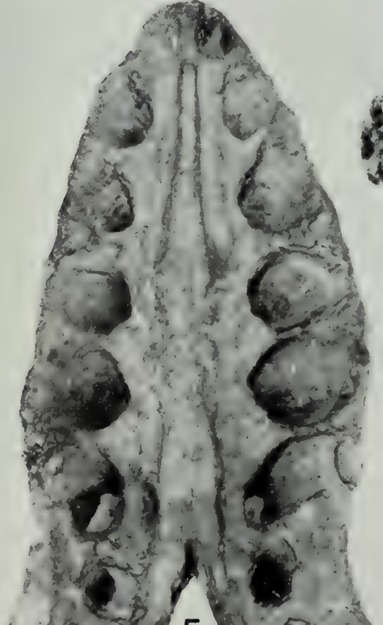
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PLATE 23

Pliosaurus andrewsi n. sp.

FIG. 1. Left scapula (R. 2437, Brit. Mus. (Nat. Hist.)) in ventral view, × $\frac{1}{3}$.

Holotype, R.3891, Brit. Mus. (Nat. Hist.).

FIG. 2. Mandible in dorsal view, × $\frac{1}{6}$.

FIGS. 3, 3*a*. Anterior cervical centrum, × $\frac{1}{2}$. 3, anterior view, 3*a*, ventral view.

FIG. 4. Left femur in dorsal view, × $\frac{1}{6}$.

FIG. 5. Epipodials and tarsus of left hind limb in ventral view, × $\frac{1}{6}$.

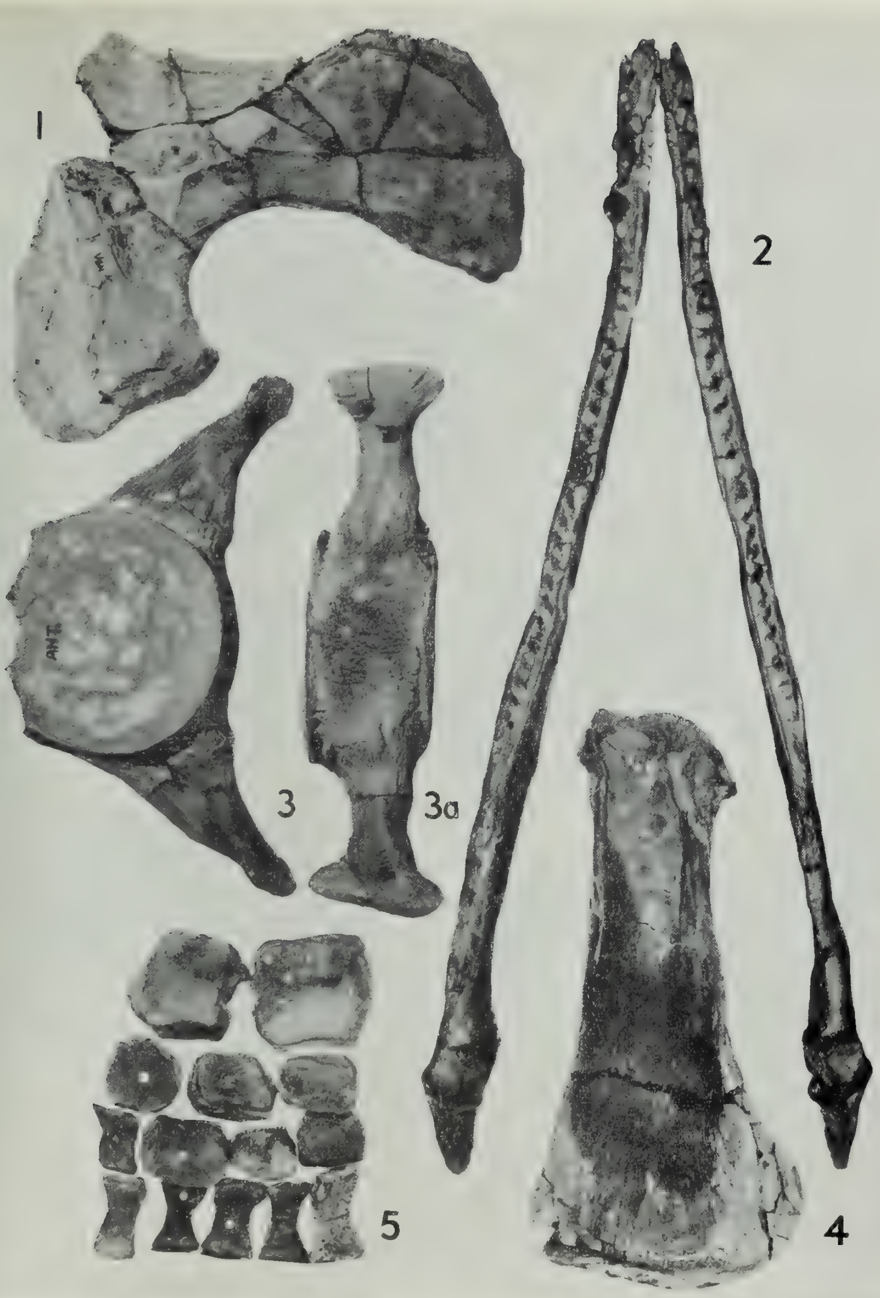
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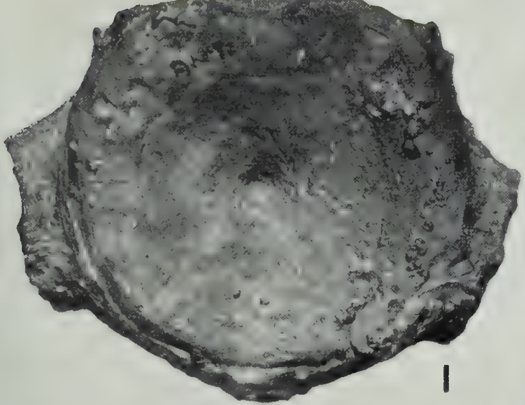
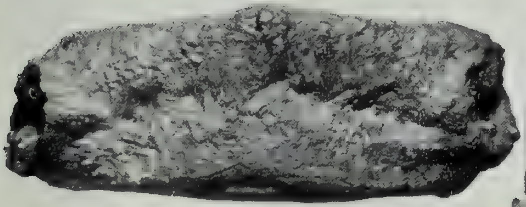
PLATE 24

Liopleurodon ferox Sauvage, associated skeleton, R.3536, Brit. Mus. (Nat. Hist.).

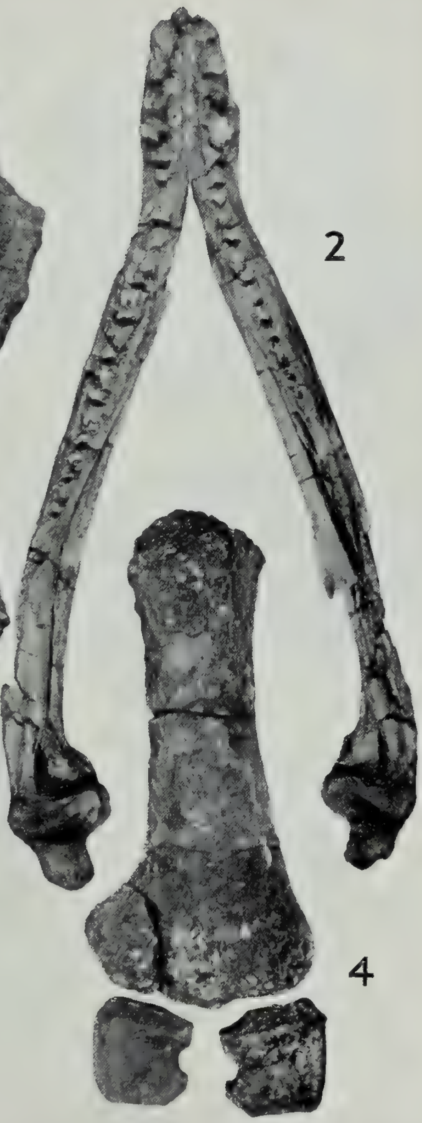
FIGS. 1, 1*a*, Anterior cervical centrum, × $\frac{3}{4}$; 1, anterior view, 1*a*, ventral view.
FIG. 2. Mandible in dorsal view, × $\frac{1}{10}$.
FIG. 3. Right scapula in ventral view, × $\frac{1}{5}$.
FIG. 4. Right femur, tibia and fibula in dorsal view, × $\frac{2}{9}$.



1



1a



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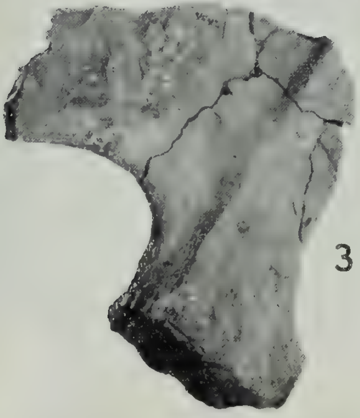
4



3

PLATE 25

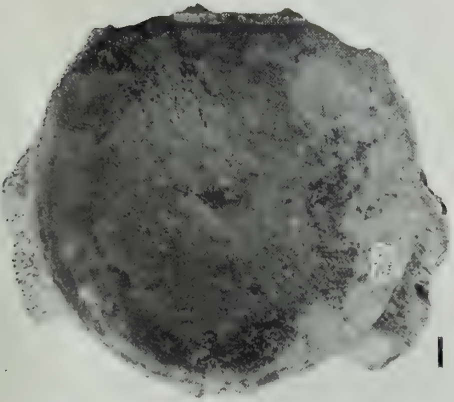
Liopleurodon pachydeirus (Seeley), holotype, J.46912. Sedgwick Museum, Cambridge.

FIGS. 1, 1*a*, Anterior cervical centrum, × $\frac{4}{5}$; 1, anterior view, 1*a*, ventral view.

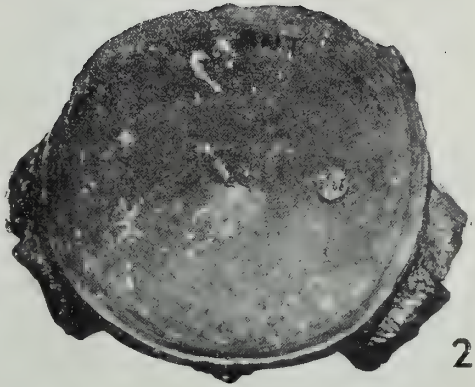
Associated skeleton, R.2446, Brit. Mus. (Nat. Hist.).

FIGS. 2–2*b*. Anterior cervical centrum, × $\frac{7}{8}$; 2, anterior view, 2*a*, ventral view, 2*b*, lateral view of left side.

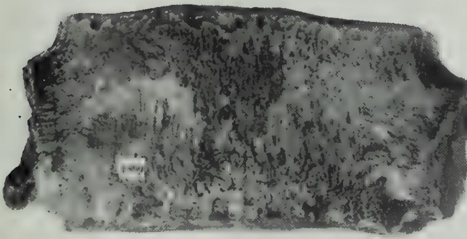
FIG. 3. Mandible, dorsal view of symphysis, × $\frac{1}{2}$.



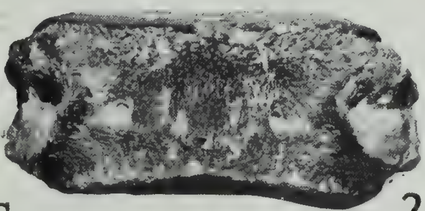
1



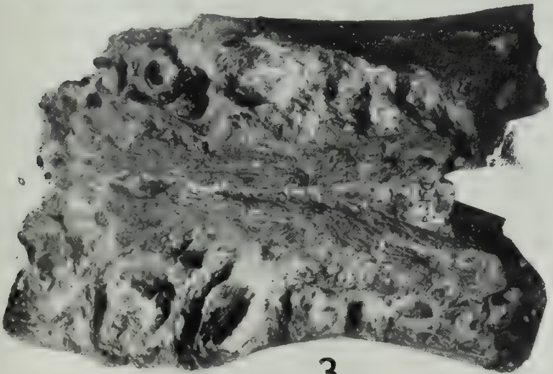
2



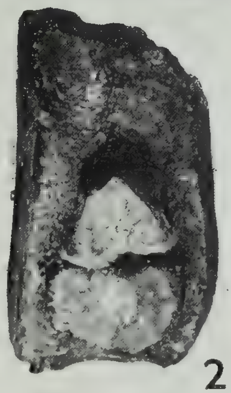
1a



2a



3

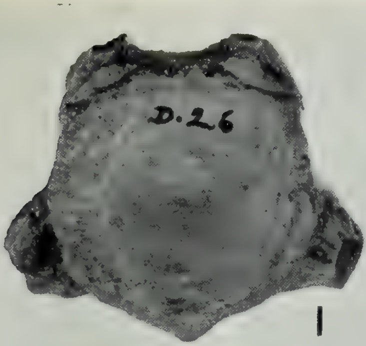


2 b

PLATE 26

Peloneustes philarchus (Seeley), holotype, J.46913, Sedgwick Museum, Cambridge.

FIGS. 1, 1*a*. Anterior cervical centrum, ×1; 1, anterior view, 1*a*, ventral view.
FIG. 2. Anterior cervical centrum, in anterior view, ×1.
FIG. 3. Fragment of crown of tooth, ×4.
FIG. 4. Mandible in dorsal view, ×½.
FIG. 5. Left scapula in ventral view, ×½.



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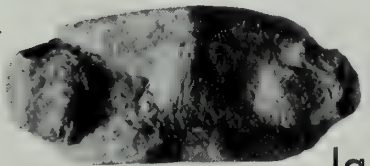

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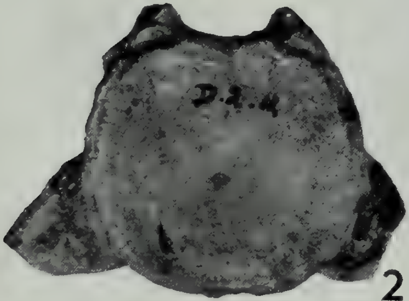

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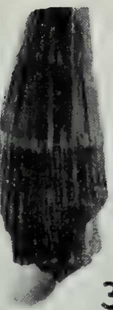

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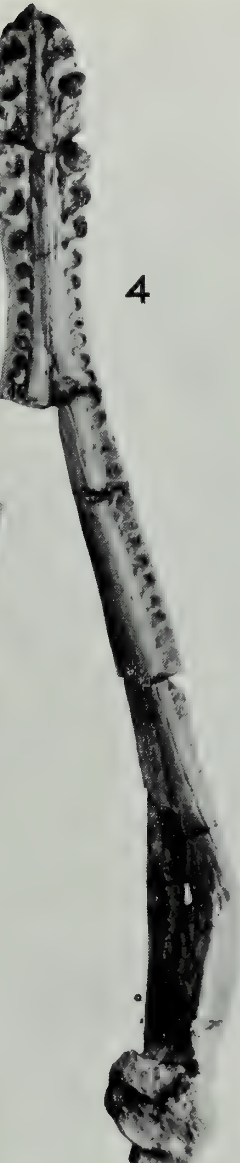

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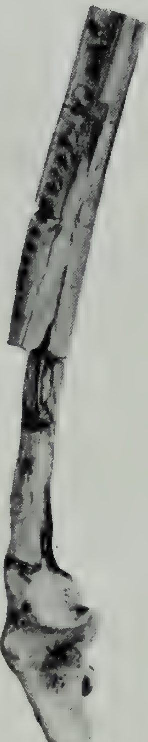
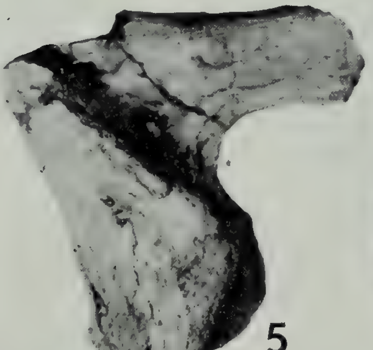




5

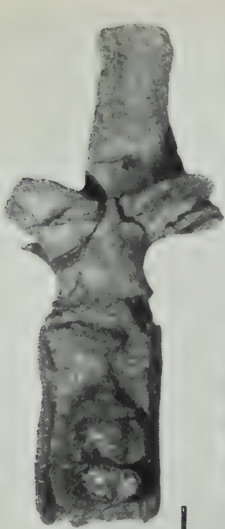
PLATE 27

Simolestes vorax Andrews, holotype, R.3319, Brit. Mus. (Nat. Hist.).

FIG. 1. Anterior cervical vertebra in lateral view, × $\frac{1}{2}$.
FIG. 2. Anterior cervical vertebra in anterior view, × $\frac{1}{2}$.
FIG. 3. Anterior cervical vertebrae in ventral view, × $\frac{1}{3}$.

Associated skeleton, R.3170, Brit.Mus. (Nat. Hist.).

FIG. 4. Mandible in dorsal view, × $\frac{1}{6}$.
FIG. 5. Left scapula in ventral view, × $\frac{1}{3}$.
FIG. 6. Left humerus in dorsal view, × $\frac{1}{3}$.



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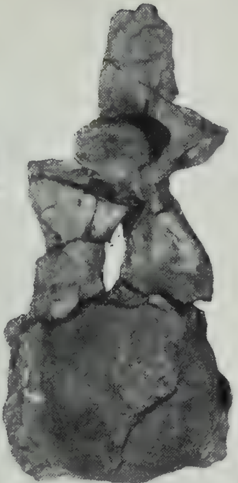

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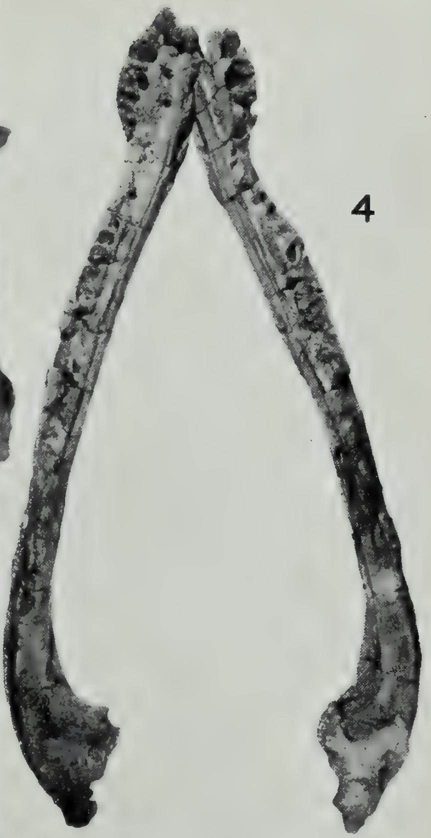

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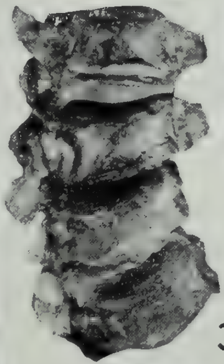

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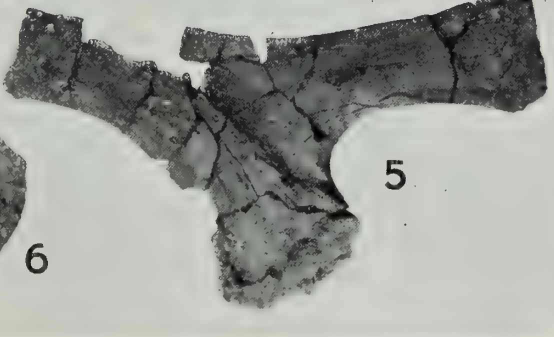

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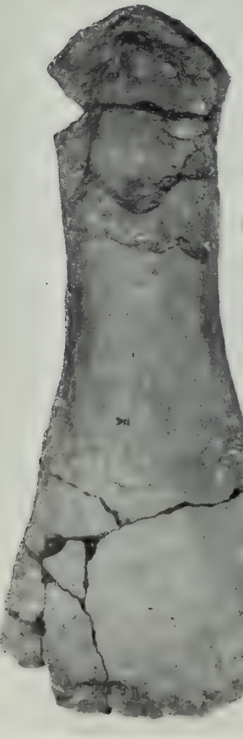


6

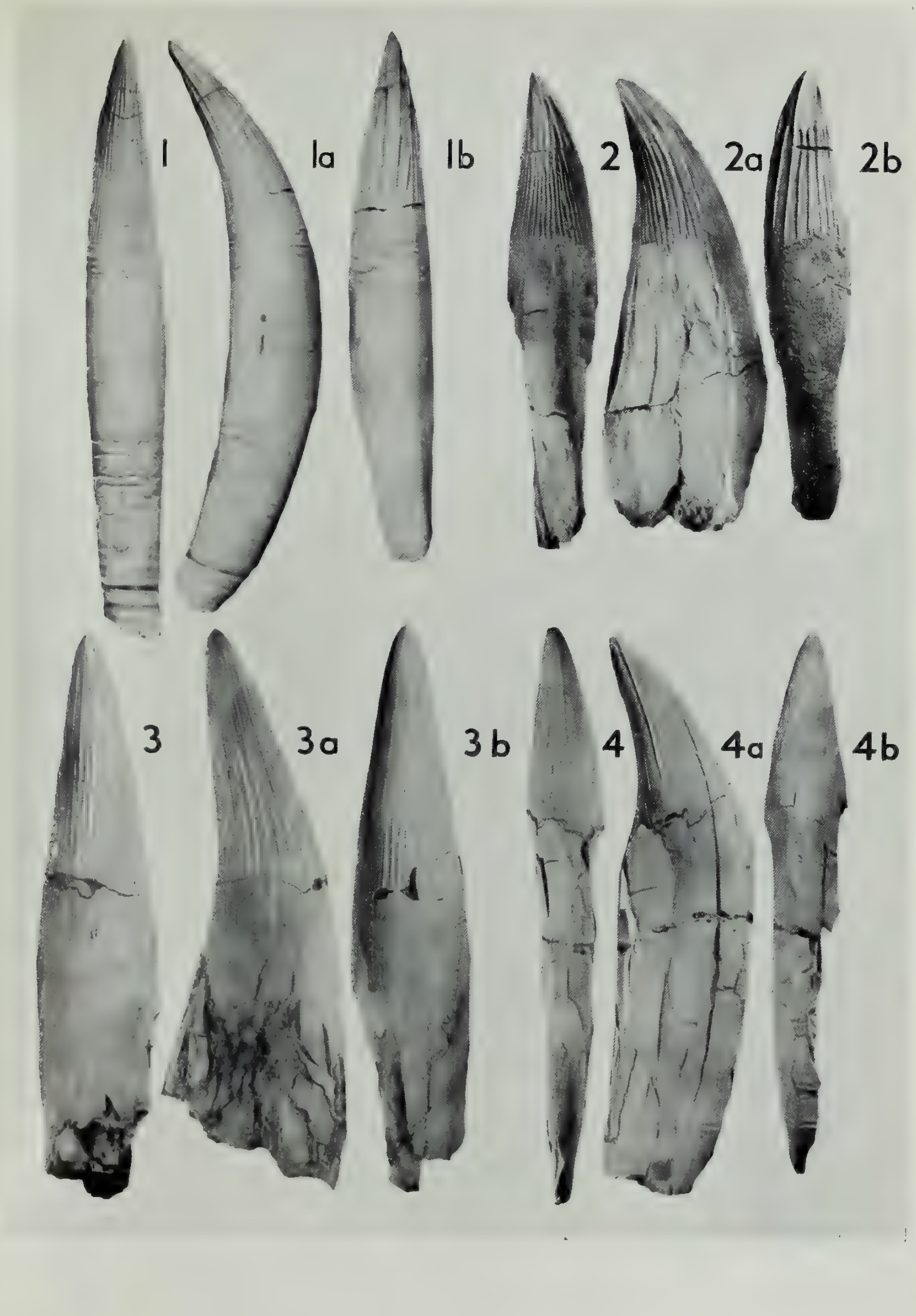
PLATE 28

FIGS. 1–1*b*. *Liopleurodon pachydeirus* (Seeley), tooth R.2446, Brit. Mus. (Nat. Hist.), × $\frac{2}{3}$; 1, internal view, 1*a*, lateral view, 1*b*, external view.

FIGS. 2–2*b*. *Liopleurodon ferox* Sauvage, tooth R.3536, Brit. Mus. (Nat. Hist.), × $\frac{2}{3}$; 2, internal view, 2*a*, lateral view, 2*b*, external view.

FIGS. 3–3*b*. *Simolestes vorax* Andrews, tooth, R.3170, Brit. Mus. (Nat. Hist.), × $\frac{2}{3}$; 3, internal view, 3*a*, lateral view, 3*b*, external view.

FIGS. 4–4*b*. *Pliosaurus andrewsi*, n. sp., tooth, R.3891, Brit. Mus. (Nat. Hist.), × $\frac{2}{3}$; 4, internal view, 4*a*, lateral view, 4*b*, external view.


1
1a
1b
2
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2b
3
3a
3b
4
4a
4b

PLANT REMAINS OF THE HENGISTBURY AND BARTON BEDS

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22 JUL 1960
NATURAL HISTORY

M. E. J. CHANDLER

BULLETIN OF
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GEOLOGY Vol. 4 No. 6
LONDON: 1960

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Pp. 191–238; *Pls.* 29–35

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PLANT REMAINS OF THE HENGISTBURY AND BARTON BEDS

By M. E. J. CHANDLER

SYNOPSIS

Plants are described from the isolated headland of Hengistbury, Hampshire and the Bartonian of Highcliff and Barton on the mainland. The geology of Hengistbury is briefly discussed and alternative suggestions as to the position of these beds with reference to the Bartonian and pre-Bartonian are summarized, especial mention in this connection being made of Mr. D. Curry's discovery of *Nummulites prestwichianus* in the Upper Hengistbury Beds. The distribution of the plants in the strata and a plant-list are given showing eighteen families, twenty-one genera. Twenty-four species are described. The large number of water plants is noted and the presence of tropical elements in *Nipa* and Mastixioideae. Almost as many species pass into the Barton or younger beds as are found in the Bournemouth Marine Beds and Highcliff Sands.

For Bartonian geology use is made of E. St. John Burton's detailed classification of the strata. Earlier records of plants are few but recent discoveries have added much to our knowledge of the Lower Bartonian plants especially of Horizon A3. The plant-list of the whole Bartonian comprises seventeen families, twenty-two genera. At least twenty-eight species are described. Again a fairly large number of water plants are present and the characteristic tropical families Capparidaceae, Anonaceae, Icacinaceae and Mastixioideae occur. A species of *Stratiotes*, common in the Bournemouth Marine and Hengistbury Beds, dies out at the top of the Bartonian. The plants alone do not appear at present to throw any new light on the relationship of the Hengistbury Beds to the coastal sequence.

INTRODUCTION

In the following pages plant remains from two sites in close geographical proximity are described. The specimens are due to the persevering efforts of Mr. D. Curry unless otherwise stated.

The deposits of Hengistbury Head, Hampshire, have been regarded by different workers as Auversian or Bartonian.

The Barton Beds of the type section at Highcliff and Barton cliffs in the same County on the mainland include the strata above the Highcliff Sands of Cliff End near Mudeford, Hampshire (see Table, Chandler, 1960 : 8))

The limits of the formation adopted are those given by E. St John Burton in 1933. The Barton Beds are truly marine and well documented with a rich fauna. They pass gradually upwards at Beckton Bunny through transition beds into the estuarine and freshwater deposits of the Lower Headon of Hordle Cliff.

I. THE HENGISTBURY BEDS

1. *Geology*

Hengistbury Head is an isolated promontory connected with the mainland only by a low neck of sand dunes in which no Tertiary strata are exposed. Consequently the exact stratigraphical relationship between the beds of the Headland and mainland is obscure. The uncertainty has not yet been resolved beyond doubt by reference to palaeontological and lithological evidence.

The lowest beds exposed are seen at the south-western end of the Headland. They consist of white, grey and black sands which have yielded to the writer a few fruits and seeds and would probably provide greater variety if persistent search were made. From them have come *Sequoia*, *Caricoidea*, *Scirpus*, *Stratiotes*, *Brasenia*, *Vitis*, *Cleyera*? and *Rhamnospermum*. It is here that Clement Reid is thought to have obtained *Nipa* (see p. 208). These dark sands extend in an easterly direction for about half a mile along the section before they disappear below sea-level. They have sometimes been regarded as the top of the Boscombe Sands but may be equivalent to the Highcliff Sands of Cliff End, near Mudeford.

Overlying these lowest sands are a Lower and an Upper Series of " Hengistbury Beds ". They are said (White, 1917 : 34) to be sub-littoral marine deposits laid down in water of moderate depth. They were regarded by Gardner (1879 : 211–217) as occurring between the Boscombe Sands and the Cliff End Beds (= Highcliff Sands) of the mainland and if so are probably Auversian. Prestwich (1849 : 43–46) referred them to the Bartonian, a correlation supported by Cowper Reed (1913 : 101–103) on the somewhat inconclusive evidence of a poorly preserved fauna in the Upper Series. The discovery of *Nummulites prestwichianus* by Mr. D. Curry (1942 : 99, pl. 3) in Hengistbury Beds 15 ft. above the basal pebble bed of the Hengistbury Series also suggests Bartonian age and may thereby afford some support for the view that the sands below the Hengistbury Series really belong to the Highcliff Beds, i.e. the beds below Burton's Horizon A1 of the Bartonian (see Curry, 1942 : 88–101).

The Lower Hengistbury Beds are dark olive-green sandy clays with much glauconite and a flint-pebble layer at the base. Their full thickness is exposed in the south-west face of the Headland. They begin to dip beneath the sea about half-way along the cliff face, and finally disappear close to the north-east angle of the Head.

The Upper Hengistbury Beds, well seen in the south-east face, are also glauconitic in places and are laminated silty clays with sandy partings. They may be pale chocolate or dark grey in colour and contain several layers of ironstones (" doggers "). Cowper Reed's fossils were found between the two highest layers of ironstone. It is noted in the Survey Memoir that five out of the six species which he identified with certainty are common to the Bracklesham and Barton Beds.

A few foraminifera were described from the clays below the ironstones by Chapman (1913 : 555). Their small dimensions and general condition suggested to him that they were the survivors of a normal " deep water ferruginous facies " in the uncongenial surroundings of the tidal estuary of a great river (p. 558). Chapman considered that the glauconite in the deposits (which is much worn) may in such circumstances have been derived from " local, disintegrated and resorted, moderately deep-water deposits ", similar to those seen in the Barton and Bracklesham Beds.

Above the Hengistbury Series are conformable yellow and white sands which have hitherto yielded no plant remains. They have generally been correlated with the Highcliff Sands of the mainland cliffs at Cliff End near Mudeford (White, 1917 : 36, 37). If, however, Prestwich, Keeping, Cowper Reed and Curry (1942) are right as to the age of the Hengistbury Beds, the sands here described would naturally be placed higher in the Bartonian Series (cf. Table, Chandler, 1960 : 8).

2. *Distribution of the Plants*

The occurrence of plants in the dark sands at the base of the section has already been mentioned.

In the Lower Hengistbury Beds, cones described here as *Pinus dixoni* (Bowerbank) Gardner were found on the foreshore in the upper part of the beds by Mr. E. St. John Burton at the south-eastern end of the Headland. It may be noted in passing that cones probably belonging to the same species were also found by him at Horizons A1, A3, D and E in the Barton Beds of Barton cliff.

In the Upper Hengistbury Beds plants were obtained by Mr. D. Curry at the following horizons : 15 ft. above the basal pebble bed of the Hengistbury Series in the *Nummulites prestwichianus* bed (the Lower Series is stated by the Geological Survey to be 12 ft. thick and the Upper Series 49 ft.) ; 19 ft. above the basal pebble bed (about 3 ft. below the lowest line of concretions or doggers) ; 25 ft. above the pebble bed (about 3 ft. above the lowest line of concretions) ; 40 ft. above the pebble bed (between the two top lines of concretions). A few specimens were labelled " between the three rows of concretions (i.e. between 22 and 40 ft. above the basal pebble bed). There appears to be no special significance in the plants found at the different levels.

Curry's plants were obtained while he was sifting for shells and *Nummulites*. The method he was obliged to employ in these clayey deposits to get them to disintegrate inevitably broke some of the carbonaceous fruits and seeds. Quite apart from this, however, many of the specimens must have been battered and fragmentary as is commonly the case where carbonaceous fossils are preserved in clay marine beds to which they may have been somewhat roughly transported. Many of these specimens are partly impregnated with pyrites and are peculiarly liable to decay. Although the yield is poor, as so often in clay beds, prolonged effort would provide at least a few additions to the list of plants at present available. On the south-eastern face, the work of collecting is now hampered by a sea-wall which prevents the sea from cutting into the face of the cliff thereby providing fresh surfaces where the plants are not rotted through long exposure to the weather. The sands in the south-western face may still be profitably worked, for they fall to pieces more readily than the tenacious sandy clay so that specimens from this locality are more easily extracted without damage.

Many of the " doggers " in the Upper Hengistbury Beds contain indeterminable fragments of battered wood. There are also occasional fruits and seeds (also noted by Prestwich, 1849 : 45–46) some of which may be recognizable although they are difficult to extract whole.

3. *List of Hengistbury Plant Remains*

Family	Genus and species	Horizon and Remarks B. Basal beds of Headland L. Lower Hengistbury Beds U. Upper Hengistbury Beds	Range summarized (O.*, Y.†)
Araucarineae	*Araucarites* sp. (? *A. sternbergi* Goeppert)	U. In Bournemouth Beds	O.Y.
Abietineae	*Pinus dixoni* (Bowerbank) Gardner	L. In Barton Beds. Cones	Y.
	Pinus sp.	U. Leaf fragments	
Taxodineae	*Sequoia couttsiae* Heer	B.U. In Lower Bagshot to Hamstead Beds	O.Y.
Potamogetonaceae	*Limnocarpus headonensis* (Gardner)	U. Water plant. Bournemouth Marine to Hamstead Beds	O.Y.
Hydrocharitaceae	*Stratiotes hantonensis* n. sp.	B.U. Water plant. Chiefly Bournemouth Marine to Bartonian Beds	O.Y.
Cyperaceae	*Scirpus lakensis* n. sp.	B. Water or subaquatic. Lower Bagshot and Bournemouth Freshwater Beds	O.
	Caricoidea obscura n. sp.	U. Water or subaquatic. Lower Bagshot to Upper Headon Beds	O.Y.
	Caricoidea sp. (? *C. obscura*)	B.	
	Caricoidea maxima n. sp.	U. Water or subaquatic	
Palmae	*Palmophyllum* sp.	U. Fan-palm leaf of type found in Lower Bagshot and Bournemouth Marine Beds	O.Y.
Nipaceae	*Nipa burtini* (Brongniart)	B. Mangrove swamps. London Clay, Bournemouth Marine Beds and a leaf ? at Hordle	O.Y. ?
Moraceae	Genus ?	U.	
Caryophyllaceae	*Hantsia pulchra* (Chandler)	U. Bournemouth Marine to Lower Headon Beds, Hordle	O.Y.
Nymphaeaceae	*Brasenia ovula* (Brongniart)	B.U. Water plant. Bournemouth Marine to Hamstead Beds	O.Y.
Burseraceae	*Palaeobursera* sp.	U. (cf. *Palaeobursera* sp. from Lower Bagshot to Lower Headon Beds, Hordle)	O.?Y.?
Vitaceae	*Vitis* n. sp.	B. Lower Bagshot Beds	O.
Theaceae	*Cleyera* ? *variabilis* (Chandler)	B.U. Woolwich, Oldhaven, London Clay, Bournemouth Freshwater to Lower Headon Beds	O.Y.
Thymeliaceae	*Daphne* sp.	U. Bournemouth Beds	O.
Epacridaceae	*Epacridicarpum mudense* n. sp.	U. Bournemouth Marine to Lower Headon Beds	O.Y.
Cornaceae (Mastixioideae)	*Mastixicarpum crassum* Chandler	U. Lower Bagshot to Lower Headon Beds	O.Y.
Symplocaceae	*Symplocos* sp. (? *S. headonensis* Chandler)	U. Lower Bagshot to Lower Headon Beds	O.?Y.?
Family ?	*Rhamnospermum bilobatum* Chandler	B.U. Water plant ? Lower Bagshot to Hamstead Beds	O.Y.
	Carpolithus cornutus n. sp.	U.	
	Carpolithus spp.	U.	

* Also in older beds than the Bartonian. † Also in Bartonian or younger beds.

4. *Analysis of the Plant List*

There appears to be no significant variation of the flora from one part of the section to another. There are eighteen families, twenty-one genera including two form-genera and twenty-four species. Almost all of the last have been found at horizons below the Bartonian (see species marked O in list). Nearly as many (marked Y in list) occur in the Barton Beds of Barton, the Lower Headon or younger beds. Of these

Nipa may be represented by leaves in the Lower Headon. Fragmentary fan-palm leaves (probably *Sabal*) occur in the horizons noted and larger fragments attributed to *Sabal* in the London Clay and Hamstead Beds. An interesting point is that the species *Stratiotes hantonensis* ranges from the Bournemouth Freshwater Beds (only one seed found) up to and including the Barton Beds of Barton cliff but it then disappears and its place is taken by *Stratiotes headonensis* Chandler in the passage beds at Long Mead End and succeeding Lower and Upper Headon Series.

The above analysis suggests that at present there is no definite evidence as to the age of the Hengistbury Beds afforded by the plants. These are disappointingly sparse as is normally the case when the flora of a period has to be derived from marine deposits. The well-known exception is the London Clay flora where the conditions of preservation are unusual and the opportunities for collecting unique. Of the small total at least eight are water or marsh plants (see list). They are presumably derived from coastal marshes, riverside bogs and lagoons or other quiet stretches of water, fresh or brackish. *Nipa, Palaeobursera* and *Mastixicarpum* are very definite tropical elements and, as often, are associated with *Sequoia couttsiae* the ubiquitous Eocene conifer, and with *Hantsia pulchra, Cleyera*? *variabilis, Symplocos headonensis* and the enigmatic *Rhamnospermum bilobatum* as well as with the water plants *Caricoidea obscura* and *Scirpus lakensis*.

II. THE BARTONIAN OF BARTON CLIFF

1. *Geology and Mode of Preservation of Plants*

The geological section in Barton cliff was described in considerable detail and the successive horizons lettered Beds A to L by E. St John Burton in 1933. The section is classical and its rich fauna is well known. While this famous fauna is a warm one it appeared to Prestwich (1857 : 131) to be less tropical in character than that of the Bracklesham Beds and it is stated that some of the large tropical shells had disappeared by Bartonian times (Gardner, Keeping & Monckton, 1888 : 584).

Plant remains, unlike animals, are scarcely known. They are sparse, poorly preserved and frequently unidentifiable, owing to a heavy encrustation of pyrites. They have obviously drifted for long in salt water and are the scanty remains of plant life from a contemporary land-surface with streams and fringing marshes draining into the Barton sea. With the exception of rare mineral casts in Bed K, the plant fossils are normally preserved as carbonaceous entities heavily impregnated with a dull lustreless pyrites mud and liable to quick decay. It is a most unfortunate circumstance that a flora so scarce should be almost impossible to preserve for any length of time. Specimens must usually be described and illustrated immediately on discovery for in a few weeks or months at latest, many may have disintegrated or seriously deteriorated. It is therefore of great importance to record and illustrate as fully as possible these ephemeral specimens ; for if the records are not made all information will be lost with the decay of the specimens themselves. Better by far careful records without specimens than no records at all. Mere names unsupported by descriptions and figures are valueless as has been demonstrated by much of Gardner's work.

2. *Old and New Discoveries of Plants*

The earlier reports of plants are few. In 1884 Gardner described and figured two very imperfect cones under the names *Pinus dixoni* (Bowerbank) (p. 66, pl. 13, fig. 5) and *P. bowerbanki* (Carruthers) (p. 68, pl. 13, fig. 6). The figures suggest that they were hardly in a state for satisfactory specific identification, a point fully realized by Gardner. Both cones were said to come from the " Middle Bagshot of Highcliff" [= Lower Barton]. He also figured from this horizon a coniferous twig which he named " *Araucaria goepperti*? Sternberg " (1883 : 59 ; 1884, pl. 13, fig. 10).

In 1887 (p. 249) he alluded to " nearly a dozen pine cones ... from the Highcliff Beds which go far to prove that there is only one variety here, indistinguishable from the *Pinus Dixoni* of Bracklesham ". He added that " along with these we have branches of apparently the Bournemouth *Araucaria*, and an important and entirely new fruit, fortunately represented by many specimens, which permit us to examine the details of their structure. These consist of twigs on which are seated in some profusion clusters of numerous sessile woody pericarps with deeply laciniate margins, giving the fruit when closed the appearance of a large burr. These enclose a nut or seed, rather smaller, but otherwise resembling that of a cucumber ... ". The specimens no longer exist and it is impossible to make a guess as to what these fruits may have been.

The richest haul of plant fossils from Barton on record was made in 1952 by D. Curry. In a letter dated January of that year he writes that A3 " consists of dark grey silty clays with few fossils. Within the clays are found thin seams of a pure silt which passes readily through a sieve without previous drying. These have obviously been produced by current action which has disturbed and re-sorted the associated clays. One result of this sorting has been the accumulation of the contained fossils in rare, but rich, pockets of small size ". Curry also states that " the fossil content of individual pockets varies considerably. Some contain a preponderance of thin lamellibranchs, others the heavier gastropods. In some there is an appreciable mixture of estuarine shells, with even rarer freshwater and land forms. Some contain a fair proportion of vegetable matter with the shells ".

The pocket from which most of the specimens hereafter described were collected was found at Highcliff where Bed A3 comes down to beach level about a quarter of a mile east of Chewton Bunny. Here Mr. Curry wrote there were " the remains of a log of wood and the shells had obviously been caught by an eddy on its lee side. There was a lot of vegetable débris among the shells and seeds were, for this horizon, unusually common ". About half a bucketful of sand was sifted. A few plants were also found by him at Horizon A2.

In the systematic descriptions which follow, the horizons (after Burton, 1933) from which specimens were obtained are indicated where possible but most collectors other than Curry have not given so much detail.

3. *List of Bartonian Plants*

Family	Genus and species	Horizon and Remarks	
Araucarineae	? *Araucarites sternbergi* Goeppert	C	Also in Bournemouth Freshwater and Marine Beds
Abietineae	*Pinus* sp. (? *P. bowerbanki* (Carruthers))	C, D	
	Pinus sp. (? *P. dixoni* (Bowerbank))	A1, A3, D, E	Also in Hengistbury Beds
Taxodineae	*Sequoia couttsiae* Heer	A3, D, L	Also in Lower Bagshot, Hengistbury to Hamstead Beds
Family ? (Coniferae)	Genus ?	A3	
Potamogetonaceae	*Limnocarpus headonensis* (Gardner)	K	Water plant. Bournemouth Marine to Hamstead Beds.
Hydrocharitaceae	*Stratiotes hantonensis* Chandler	A3	Water plant. Bournemouth Marine to Barton Beds. Rare in Bournemouth Freshwater Beds.
	Stratiotes headonensis Chandler	L	Water plant. Lower and Upper Headon Beds.
Cyperaceae	*Caricoidea obscura* Chandler	A3	Water or subaquatic. Lower Bagshot to Upper Headon Beds.
Nymphaeaceae	*Brasenia ovula* (Brongniart)	A3, K, L	Water plant. Bournemouth Marine to Hamstead Beds.
Capparidaceae ? or Theaceae ?	Genus ?	A3	Family in Lower Bagshot and Bournemouth Freshwater Beds.
Anonaceae	*Anonaspermum* sp.	Bartonian horizon ?	Family in London Clay and Bournemouth Freshwater Beds.
Rutaceae	*Rutaspermum* sp.	Bartonian horizon ?	Genus London Clay to Colwell.
	Rutaspermum sp.	A2	
Icacinaceae	*Icacinicarya pygmaea* n. sp.	A3	Family Palaeocene to Headon Beds.
	Icacinicarya bartonensis n. sp.	K	
	Genus ? (? *Natsiatum eocenicum* Chandler)	A3	
	Stizocarya sp.	Middle Bartonian	London Clay (to Headon ?).
Theaceae	*Hordwellia crassisperma* (Chandler)	A3	Lower Bagshot to Upper Headon Beds.
	Cleyera ? *variabilis* (Chandler)	A3	Bournemouth Freshwater to Lower Headon Beds.
	Cleyera ? *bartonensis* n. sp.	A3	
Thymeliaceae	? *Daphne* sp.	A3	Hengistbury and Bournemouth Marine Beds.
	Genus ?	A3	
Lythraceae	*Decodon gibbosus* (E. M. Reid)	A3	Subaquatic. Upper Headon, Pliocene.
	Diclidocarya minor n. sp.	A3	Subaquatic. Genus German Brown Coal.
	Palaeolythrum bournense n. sp.	A3	Subaquatic. Bournemouth Freshwater to Upper Headon and Bovey.
Cornaceae (Mastixioideae)	*Eomastixia rugosa* (Zenker)	Lower and Middle Bartonian	Lower Bagshot to Lower Headon Beds.
Epacridaceae	*Epacridicarpum headonense* n.sp.	A3	Bournemouth Marine, Hengistbury, Lower Headon, ? Upper Headon Beds.
	?*Epacridicarpum mudense* Chandler	A3	Bournemouth Marine, Hengistbury, Lower Headon Beds.
Symplocaceae	*Symplocos* sp.	A3	
Family ?	*Rhamnospermum bilobatum* Chandler	A3, L	Probably water plant. Lower Bagshot to Hamstead Beds.
	Carpolithus spp.	Lower Bartonian horizon ? A3	

4. *Analysis of the Flora and Range of its Species*

Seventeen families have been recognized up to date with twenty-two genera including such form-genera as *Icacinicarya* and *Epacridicarpum.* There are at least twenty-eight distinct species some of which cannot be named for lack of sufficient data to define them and it may be noted that eleven are probably true water plants or subaquatic but these two groups, as a rule, give little information as to climate. The presence, however, of the families Capparidaceae, Anonaceae, Icacinaceae (with four representatives) and Mastixioideae indicates a considerable measure of warmth. *Stizocarya* is itself a London Clay genus. *Eomastixia* has been traced from the Pipe-clay Series of Dorset, through the Bournemouth Freshwater and Marine Beds up to the Lower Headon, but not, so far, into younger beds.

In addition to these definitely warmth-loving plants the following are associated with warm floras at other horizons: *Araucarites sternbergi, Sequoia couttsiae, Caricoidea obscura, Hordwellia crassisperma, Cleyera? variabilis, Palaeolythrum bournense,* and the puzzling *Rhamnospermum bilobatum.* Two of these, *Sequoia* and *Rhamnospermum* continue to thrive in the Bembridge and Hamstead Beds where some cooling of the climate may perhaps have occurred.

In addition the Barton, Cliff End and Bournemouth Marine Beds share a number of species which are wholly or almost absent at horizons below the Marine Beds so far as present knowledge goes. Thus the water plants *Brasenia ovula* and *Limnocarpus headonensis* are found almost universally in the Tertiary plant beds of southern England but only from the Bournemouth Marine Beds onward apart from a single endocarp of *Limnocarpus* from the Cuisian of Whitecliff Bay, Isle of Wight. Again *Microdiptera parva* supersedes, at this same horizon an older, larger species, awaiting publication from the Bournemouth Freshwater Beds. These three species all survive into the Oligocene. In like manner the Epacridaceae make their first recorded British appearance in the coast section in the Bournemouth Marine Beds and are known also from the Highcliff Sands at Cliff End, near Mudeford as well as from the Hengistbury Beds, Lower Headon, and Upper Headon of Colwell. The range of *Stratiotes hantonensis* is mentioned on p. 199. It is essentially a Bournemouth Marine to Bartonian species. These records suggest that the passage from Bournemouth Freshwater to Bournemouth Marine Beds may mark a phase in the development of the Eocene flora.

The genus *Decodon* calls for special mention for up to date it is in the Barton Beds that it is first found in England. The species *D. gibbosus* (E. M. Reid) was based on Pliocene seeds from Pont-de-Gail (Cantal), France, and has now been recognized also at an intermediate horizon in the Upper Headon of Colwell.

5. *Concluding Remarks*

While (unpublished) knowledge of the floras of the Bournemouth Marine Beds and Highcliff Sands is fuller than that of the Barton and Hengistbury floras, there is, on the whole, no significant change between the oldest and youngest of these beds. It is therefore impossible at present to differentiate between these successive stages on the basis of the plants alone. Hence it follows that there can be no grounds for relating the Hengistbury flora to that of the Highcliff Sands or Bournemouth Marine Beds on the one hand rather than to the Barton flora on the other. This opinion agrees with the one expressed on p. 197 after a study of the Hengistbury plants. Detailed consideration of the Barton flora also confirms that, in the present stage of knowledge, the plants have little to contribute to the problem of the age of the much discussed Hengistbury Beds.

The author's warmest thanks are due to Dr. K. I. M. Chesters and Mr. F. M. Wonnacott for much valued help and criticism in the prepation of this paper.

SYSTEMATIC DESCRIPTIONS

1. *Plant Remains from Hengistbury Head, Hampshire*

GYMNOSPERMAE

Order CONIFERALES

Family ARAUCARINAE

Genus ***ARAUCARITES*** Presl 1838

Araucarites sp. (? ***Araucarites sternbergi*** Goeppert)

(Pl. 29, figs. 1–3)

1850. *Araucarites sternbergii* Goeppert, pl. 44, fig. 1.
1883. ? *Araucarites goepperti* (Sternberg) : Gardner, p. 59.
1884. ? *Araucarites goepperti* (Sternberg) : Gardner, pl. 12, fig. 10.

The species described by Gardner from the Bournemouth Beds appears to be represented by small fragments of twig, usually pyritized and much corroded. The reasons for assigning the Bournemouth material to *A. sternbergi* Goepp. are given by Florin in Reid & Chandler (1926 : 50).

One poorly preserved twig from the Upper Hengistbury Beds showing long falcate leaves was found as an impression in an ironstone nodule (V.36426). Carbonaceous twigs were isolated from the clays between the concretions or " doggers ". One of these with spirally arranged leaves shows slightly incurved tips (Pl. 29, fig. 1). It, and a thicker twig, were sacrificed in preparing cuticle (slides V.36349, V.36350, V.36351). The tiny fragments show characteristics of *Araucarites* rather than of *Sequoia couttsiae*, e.g. in the large stomata (length of aperture 0·04–0·05 mm.) and in the coarseness and large size of the epidermal cells. Outside the stomatal bands the ordinary epidermal cells have a tendency to narrow towards their ends (slide V.36351) as in *A. sternbergi* from Bournemouth, inside they are frequently equiaxial.

The cells bear scattered simple pits. One fragment apparently from the ventral surface of the leaf shows several transversely oriented stomata in a longitudinal row. Two of these are separated by four transversely elongate and aligned epidermal cells between their auxiliaries. On what appears to be a fragment of the dorsal surface the stomata are mainly longitudinally aligned. On the decurrent basal regions of the leaf they are most frequently oblique (slide V.36349). V.36350 shows a marginal decurrent ventral fragment with transverse and oblique stomata.

A long falcate detached leaf (Pl. 29, fig. 3) was destroyed in an unsuccessful attempt to prepare cuticle.

Family Abietineae

Genus ***PINUS*** Linnaeus

Pinus dixoni (Bowerbank) Gardner

(Pl. 29, figs. 12, 13 ; Pl. 30, figs. 14, 15)

1850. ? *Pinites dixoni* Bowerbank *in* Dixon, , p. 84, pl. 9, fig. 3.
1878. ? *Pinites dixoni* Bowerbank : Carruthers *in* Dixon, p. 162.
1884. *Pinus dixoni* (Bowerbank) Gardner, p. 66, pl. 13, figs. 1, 2, 5, 8 ; text-fig. 27.

Amended diagnosis. Cones elongate-ovoid, scales with rhomboidal apophyses with prolonged umbo and transverse carina, apophyses ornamented with divergent striae. Dimensions of apophyses about 12·5 × 7 mm. Length of cone (not quite complete), 7·5 cm. ; breadth (much compressed), 3·5 cm.

Neotype. A cone imperfect at the base. Brit. Mus. (N.H.), No. V.36352.

Description. *Cone* : Elongate-ovoid (incomplete at the base, much compressed in fossilization). Scales with rhomboidal apophyses the larger of which are about 12·5 mm. in transverse diameter by about 7 mm. in height, with a dorsal prolonged umbo and a transverse carina ; on the apophyses are divergent striae especially conspicuous below the carina. Length of cone preserved, 7·5 cm. ; breadth, 3·5 cm.

Remarks and affinities. Two cones, one (V.36352) with about seventy-six scales preserved, imperfect at the base, the other (V.36353) much more incomplete. Both were found by E. St John Burton. In the dimensions and form of the cone, and in the character and size of the apophyses, there is a close resemblance to a specimen of *Pinus dixoni* from Bracklesham figured by Gardner in 1884 (pl. 13, figs. 1, 2). Gardner later stated (1887 : 249) that he had also found a dozen cones indistinguishable from *P. dixoni* in the Highcliff Beds (Lower Bartonian), but only a fragmentary cone from Highcliff was figured by him under this specific name (1884, pl. 13, fig. 5). It may be presumed that these cones quickly shed their scales, as is liable to happen when they are released from the matrix, so that they could not be illustrated. A similar cone (now decayed) with similar scales was found by E. St John Burton in the Middle Bartonian (Horizon D) in Barton cliffs (see p. 220, Pl. 33 figs. 75–79).

Gardner also referred two cones from the Bembridge Marls of Gurnet Bay to this species (1884 : 67, pl. 13, fig. 4) but the apophyses were not well shown and the specific identity cannot be satisfactorily established unless (as is again possible) the apophyses were preserved at the time of the discovery and decayed before the plate was drawn (cf. Reid & Chandler, 1926 : 53, 54).

Pinus sp.

(Pl. 29, figs. 4–11)

Fragments of pine-needles occur throughout the Upper Hengistbury Beds. They have been collected at unspecified horizons between the three rows of concretions (V.36354) and at 15 (V.36355), 25 (V.36356, V.36357, V.36359, V.36360) and 40 ft. (V.36358) above the basal pebble bed. The longest fragment measures 5 mm. and is 1·25 mm. broad. One surface of the needles is always gently convex with several clearly defined lines of close-set stomata. There may be five, six, or seven lines, but usually there are six or seven (Pl. 29, figs. 5, 9, 10). The other surface is more or less sharply ridged or angled longitudinally, the ridge being asymmetrically placed in most fragments and flanked by a more or less conspicuous furrow on each side beyond which the surface flattens out, but there are less conspicuous subsidiary ridges sometimes visible and clearly seen in the cuticle. There is usually one row of stomata on the ridge as in the specimens figured in Pl. 29, figs. 8, 11. Sometimes there are two contiguous rows in parts of the ridge.

A leaf with seventeen stomatal rows on the convex surface shows two contiguous rows in the hollow of the opposite surface on the broader side and two on the flat region beyond it, with at least four rows on the narrower side of the conspicuous angle (V.36364) (Pl. 29, fig. 11).

A leaf with six stomatal rows on the convex surface shows one row in each hollow of the opposite surface and three rows beyond the hollow on the more flattened region of the leaf.

In another fragment with six rows on the convex surface, there are three rows of stomata flanking the ridge on each side on the opposite surface and on one side of it one of these rows lies in the hollow, all other rows being on the flattened part of the surface.

A fragment with seven rows of stomata (two of which were discontinuous) on the convex surface has three rows on each side of the ridge on the opposite surface two rows being contiguous on each side of the ridge while on the ridge itself the one row is asymmetrically placed.

A fragment with six rows on the convex surface shows on the opposite surface, three rows on one side of the rib with one row on the rib itself and one row (or possibly two adjacent rows not clearly distinguishable) on the opposite side of the rib on the flat part and one in the hollow (Pl. 29, fig. 8).

Attempts were made to prepare cuticle fragments. A few poor fragments were obtained but they at least show some definite features. Where two rows of stomata are continguous lateral auxiliary cells may be shared by stomata of adjacent rows. Otherwise there may be several rows of ordinary epidermal cells between the rows. Contiguous stomata in the same row may sometimes share a polar auxiliary cell. Auxiliary cells varied (where they could be counted) from 10–14. There are two polar auxiliary cells and four, five, or six lateral auxiliary cells on each side of the pore. The lateral auxiliary cells are isodiametric and densely cuticularized. There is a most conspicuous ring of cuticle on the inner edge of these cells where they join the guard cells. Stomatal pores are about 0·067 mm. in diameter, sometimes 0·08 × 0·05 mm. The lateral auxiliary cells are 0·013–0·014 mm. in diameter. The ordinary epidermal cells of the surface show a superficial reticulate thickening. In places the walls are almost imperceptibly sinuous. In other places they are slightly sinuous. The cells which form the ridges of the surface are larger than the other cells, sometimes square-ended and about 0·03–0·036 mm. broad. The ridges bear short blunt teeth situated about 0·11–0·135 mm. apart (V.36359).

The needles probably belong to a single species. They seem to be specifically distinct from fragments described from Cliff End which (although their preservation made it impossible to prepare cuticle) appear to show a larger number of rows of stomata on the convex surface and simpler ridging of the opposite surface with a broader flatter area flanking the ridge. The character of the stomata with as many as fourteen auxiliary cells and the sharing of lateral auxiliary cells where stomatal rows are contiguous as well as the short isodiametric character of the lateral auxiliaries all indicate the section *Diploxylon* of Koehne for the Hengistbury species.

There is no evidence of connection with the cones described on p. 202 although possibly the two may belong to the same species.

Family TAXODINEAE

Genus ***SEQUOIA*** Endlicher

Sequoia couttsiae Heer

See references, Chandler, 1957, p. 82.

Small twig fragments from Hengistbury are to be figured in the Lower Bagshot monograph where the species *S. couttsiae* is fully described. Two were collected between the three lines of concretions (" doggers ") in the Upper Hengistbury Series. One twig from the lowest dark sands at the western end of the Head was destroyed in an attempt to prepare cuticle. The solitary slide (V.36365) is very poor but shows tiny fragments in a much decayed condition. Among them are several strips of ventral decurrent cuticle at the base of the leaf showing large cells and a few oblique stomata with auxiliary cells arranged end to end. Poor scraps from the base of the ventral free surface show the middle part and parts of the marginal flanges where they were attached to the twig.

ANGIOSPERMAE

Class MONOCOTYLEDONES

Family POTAMOGETONACEAE

Genus ***LIMNOCARPUS*** C. Reid emend. Reid & Chandler, 1926 : 68

Limnocarpus headonensis (Gardner)

(Pl. 30, figs. 16, 17)

1888. *Carpolithes headonensis* Gardner, p. 420, pl. 3, fig. 30.
1926. *Limnocarpus headonensis* (Gardner) : Reid & Chandler, p. 70, pl. 4, figs. 1–3. See also for other references.

One obovoid locule-cast from which most of the carpel wall has been abraded. The cast shows the curved form and oblique excentric process around which it is curved situated at about one-third of the length from the apex. The style base can be seen at the upper end of the ventral margin. The cast of the germination valve shows that it did not reach the style. Although the removal of the external surface has obscured or destroyed any evidence of external rugosities the size and proportions of this specimen indicate that it belongs to *Limnocarpus headonensis*, a species of frequent occurrence in both older and younger beds of the coast section. In the mode of preservation it agrees with a specimen from the Cuisian of Whitecliff Bay, Isle of Wight (awaiting publication) and with endocarps from Bed K of the Bartonian at Beckton Bunny (p. 222 Pl. 33, figs. 84–86). Length of cast, 1·5 mm. ; breadth, 1·25 mm. ; thickness, 1 mm.

Family HYDROCHARITACEAE

Genus ***STRATIOTES*** Linnaeus

Stratiotes hantonensis n. sp.

(Pl. 30, figs. 18–25)

DIAGNOSIS. Seed suboval, hooked or sigmoidal in outline, much inflated (although often flattened as the result of fossilization). Keel rather narrow and inconspicuous ; collar rough and nodular in unworn seeds (smooth, rounded and smaller in abraded seeds). Testa woody, ornamented with discontinuous pronounced longitudinal ridges and conspicuous pits (when unworn). Micropyle basal or sub-basal, straight or oblique, hilum from about one-third to one-half of the length from the base in hooked seeds, near the apex (as preserved) in sigmoidal seeds. Raphe marginal to the apex then transverse in hooked seeds, apical and transverse (as preserved) in sigmoidal seeds. Length usually about 2·5–3·5 mm. rarely larger. Largest seed seen : length, 4 mm. ; breadth, 2·25 mm.

HOLOTYPE. Brit. Mus. (N.H.), No. V.36484 from the Bournemouth Marine Beds, Southbourne, Hampshire, awaiting publication.

The species is based on better-preserved seeds from Bournemouth Marine Beds the account of which awaits publication. It includes full details of the characters and a discussion of the relationship of these seeds. The Hengistbury seeds, like those from Bournemouth, are suboval, sometimes hooked at the base, sometimes sigmoidal in outline, frequently much inflated although in many instances flattened as the result of fossilization. Keel sharply or scarcely differentiated from the body, merging into the collar at the base. Collar often conspicuous, frequently smooth, sometimes clearly differentiated from the body by a constriction. Testa ornamented externally by conspicuous discontinuous longitudinal ridges and large pits but the appearance varies considerably with the degree of abrasion. Hilum on the keeled margin varying in position from half to one-third from the base in hooked seeds, near the apex at the extremity of the hook or beak in sigmoidal seeds. Raphe marginal to the apex in hooked seeds where it passes directly across the keel to the apical chalaza, remaining only as a short transverse canal near the apex of the keel in sigmoidal seeds. Digitate cells of the interior of the keel elongate parallel to the length of the seed, sometimes sinuous. Dimensions of some typical seeds are 3 × 1·75 mm. ; 3·1 × 1·6 mm. ; 3·25 × 2·5 mm. ; 3·6 × 2·1 mm. ; 4·25 × 2·25 mm.

REMARKS. The seeds can be matched exactly in size and characteristics among the seeds of *Stratiotes hantonensis* from the Bournemouth Marine Beds and Highcliff Sands.

Family CYPERACEAE

Genus ***SCIRPUS*** (Linn.)

Scirpus lakensis n. sp.

(Pl. 30, fig. 26)

DIAGNOSIS. Fruit narrow-oburceolate in outline with conspicuous basal neck and long terminal persistent style. Surface longitudinally ridged, cells hexagonal, transversely elongate, arranged in longitudinal rows between the ridges (broken-down cell walls often persisting as lines of bristles along the ridges in abraded specimens). Length of fruit, 1·4–2·5 mm. ; breadth, 0·65–0·8 mm. Cells as much as 0·1 × 0·3 mm. in diameter.

HOLOTYPE. Brit. Mus. (N.H.), No. V.40397 from Lower Bagshot, Lake, Dorset, awaiting publication.

REMARKS. The species is based on beautiful material from Lower Bagshot Beds. Only three much abraded fruits have been found at Hengistbury. One (V.36378) is typical, attenuated to the long tapering style with basal neck. Only the inner yellow shining translucent coat is preserved but it shows the longitudinal ridges and between them remains of the transverse hexagonal cells in regular longitudinal rows. Two others (V.36379) are even more worn. Length of best specimen, 1·4 mm. ; breadth, 0·7 mm.

Genus *CARICOIDEA* Chandler, 1957 : 86

Caricoidea obscura n. sp.

(Pl. 30, figs. 27–33)

Diagnosis. Fruit sub-obovoid, rounded at the apex, truncate at the base, formed of thick spongy parenchyma, surface with longitudinally elongate digitate cells. Length, 1–2 mm. ; breadth about 0·5–1·75 mm. Endocarp obovoid, narrowing gradually to the truncate base, mucronate at the apex. Length about 0·95–1·3 mm. Locule lining longitudinally ridged formed of longitudinal cells. Testa hyaline of transversely aligned cells.

Holotype. Brit. Mus. (N.H.), No. V.40407 from the Highcliff Sands, Cliff End, near Mudeford, Hampshire, awaiting publication.

Remarks. The species is not uncommon at Hengistbury and is represented by both fruits and endocarps. One specimen is represented by an endocarp still adhering to a fragment of fruit. The complete fruits show the typical, laterally angled sub-obovoid form with basal aperture and thick close-textured parenchymatous wall. The endocarps, when isolated, have a distinctly mucronate apex and narrow well-marked neck (cf. V.36381, V.36382 and V.36386). The specimen V.36385 (Pl. 30, fig. 33) may be immature. It is small (1·8 × 1·4 mm.) but is important as it shows the epidermal layer with longitudinally elongate digitate cells. Length of fruit about 2 mm. ; breadth, 1·5–1·75 mm. Length of endocarp, 1·4–1·5 mm. ; breadth, 1·1–1·3 mm.

Caricoidea sp. (?*Caricoidea obscura* Chandler)

(Pl. 30, fig. 34)

An obovoid endocarp, pointed, almost mucronate, at the apex, gradually narrowed to the truncate base to which remains of the fruit adhere giving a superficial appearance of an expanding neck. The specimen is much compressed so that its structure is somewhat obscure. It may be a crushed specimen of *C. obscura*.

Caricoidea maxima n. sp.

(Pl. 31, fig. 35)

Diagnosis. Fruit obovoid, truncate at the base with deep depression. Length about 4·25 mm. ; breadth about 2·75 mm.

Holotype. Brit. Mus. (N.H.), No. V.36388.

Description. *Fruit*: Sub-obovoid, somewhat flattened (probably original), truncate at the base, with a basin-shaped depression (obscured by adherent sand).

Apex somewhat pointed. External surface abraded so that the epicarp layer is not preserved. Wall compact, formed of equiaxial cells. Endocarp not seen. Length of fruit, 4·25 mm.; maximum breadth, 2·75 mm.

REMARKS. One fruit somewhat battered, abraded, and distorted. It is remarkable for its large size as compared with the other species and has therefore been given the specific name *C. maxima*.

Family PALMAE

Genus ***PALMOPHYLLUM*** Conwentz

Palmophyllum sp.

(Pl. 31, figs. 36, 37)

A tiny fragment of the leaf of a small fan-palm showing part of five pinnules near their origin still attached to a piece of the rachis. It is exactly comparable with fragmentary palm leaves from the Lignites above the Boscombe Sands at Southbourne awaiting publication. Surface cells on the pinnae are longitudinally aligned in rows, rectangular or almost square, about 0·01 mm. in diameter. The cells on the Southbourne leaf fragments were not preserved owing to the abrasion of the surface. There can be little doubt that the fragments from the two localities belong to the same species. The fragment from Hengistbury measures 6 × 3·5 mm. and is of *Sabal* type.

Family NIPACEAE

Genus ***NIPA*** Thunberg

Nipa burtini (Brongniart)

1894. *Nipadites parkinsonis* (Brongniart): Rendle, p. 150.
1917. *Nipadites parkinsoni* (Brongniart): White, p. 34.
1933. *Nipa burtini* (Brongniart): Reid & Chandler, pp. 119, 128.

The specimen was a sandy cast like those from Honeycomb Chine. It was never figured but is mentioned by Rendle (1894). Reid & Chandler considered that there were no grounds for creating more than one species out of the British material which should all be referred to *N. burtini* (Brongniart).

Class DICOTYLEDONES

Family MORACEAE

Genus ?

(Pl. 31, fig. 38)

DESCRIPTION. A much compressed fruit (now broken) shows the typical stylar end of an endocarp of Moraceae. The fruit is suboval in outline, one margin being more markedly convex than the other, and is narrowed to the terminal style. The attachment and placenta are closely adjacent to the style. Both style and attachment are marked by conspicuous marginal prominences, the attachment being made conspicuous by the recurved remains of the funicle. Length, 2 mm.; breadth, 1.25 mm.

The form and adjacent stylar and funicular prominences at the apex indicate relationship with Moraceae. The specimen is more elongate-oval in outline than *Moroidea boveyana* Chandler (1957 : 95, pl. 13, fig. 74) and its surface is more rugose.

Order CENTROSPERMAE

Family CARYOPHYLLACEAE

Genus ***HANTSIA*** nov.

DIAGNOSIS. Seeds with curved embryo belonging to the Centrospermae; large rimmed hilum between the limbs. Testa with smooth or tubercled digitate cells externally. Inner integument of small uniform equiaxial cells.

TYPE SPECIES. *Hantsia pulchra* (Chandler).

Hantsia pulchra (Chandler)

(Pl. 31, fig. 39)

1925. *Corydalis pulchra* Chandler, p. 25, pl. 2, fig. 10*a*, *b*.

HOLOTYPE. Brit. Mus. (N.H.), No. V.20051 from Lower Headon of Hordle, Hampshire.

For reasons discussed in a work on the Lower Headon awaiting publication the species has been transferred to the family Caryophyllaceae and to a new genus *Hantsia*. In the same volume new material from the type locality (Lower Headon, Hordle) is compared with material from other new horizons.

DESCRIPTION. A much distorted and broken seed from Hengistbury shows the transversely oboval campylotropous form. Between the unequal limbs lay a large rimmed aperture in the better preserved material from other deposits but not here preserved. The surface, which is black and shining bears large rounded tubercles each arising from a cell or area with finely toothed margin, one of the characteristics which suggest affinity with Caryophyllaceae and not seen in the original Hordle material. Diameter of tubercled areas about 0·05–0·14 mm. On the broken surfaces the columnar character of the testa is clear, part of the columnar effect being due to the toothed " cell " margins, the teeth forming ridges on the sides of the " cells ". No inner integument can be seen in this specimen. Diameters of distorted seed, 2·3 × 1·75 mm.

Family NYMPHAEACEAE

Genus ***BRASENIA*** Schreber

Brasenia ovula (Brongniart)

(Pl. 31, figs. 40, 41)

1926. *Brasenia ovula* (Brongniart) : Reid & Chandler, p. 99, pl. 6, figs. 15–18. See also for other references.

The typical shining ovoid seeds of this species occur throughout the strata at Hengistbury Head. They show the embryotega and the columnar section and clawed or digitate surface cells characteristic of the species as well as variation of form and size. Two specimens here figured measure 2·5 × 2 mm. and 2·25 × 1·25 mm. respectively. Both were much compressed in fossilization. In addition seeds were preserved at 19 ft. and 25 ft. above the basal pebble bed (V.36394, V.36395).

Family BURSERACEAE

Genus ***PALAEOBURSERA*** Chandler, 1960 : 202

Palaeobursera sp.

(Pl. 31, figs. 42, 43)

DESCRIPTION. A pyrene suboval in outline, much compressed dorsiventrally in fossilization but the dorsal surface must originally have been slightly convex. Facets of the ventral surface meeting to form a median broad longitudinal angle extending throughout the length, angle pierced at a short distance below the middle by the transverse aperture making the point of entry of the funicle. Germination valve occupying the upper three-quarters of the dorsal surface obscured partly by adherent tissue (of the fruit?). Wall formed superficially of equiaxial cells about 0·027 mm. in diameter. Length of pyrene, 2 mm. ; breadth, 1·25 mm.

REMARKS. The solitary specimen closely resembles a species from the Lower Bagshot awaiting publication under the name *P. lakensis* but is somewhat smaller than that species, possibly due to shrinkage. In its compressed state it is not possible to estimate the number of pyrenes in the fruit.

Family VITACEAE

Genus ***VITIS*** (Tourn.) Linnaeus

Vitis sp.

(Pl. 31, figs. 44, 45)

DESCRIPTION. *Seed :* Broadly obovate in outline, now dorsiventrally flattened, originally somewhat inflated, markedly stipitate with a thick but definite stipitation, not channelled at the apex, contours smooth and rounded. Dorsal surface originally convex (now crushed almost flat), chalaza narrow oval situated rather above the middle, not appreciably sunk, without conspicuous furrows above or below. Ventral surface originally faceted (now flattened) with parallel rounded raphe ridge. Ventral infolds deep, broad, short, not reaching the base, sub-parallel with a slight tendency to diverge and broaden upwards, scarcely extending to a quarter of the length of the seed from the apex. Cells of the testa equiaxial, concave, about 0·018 mm. in diameter. Thickness of testa 0·165 mm. Length of seed, 3·25 mm.; breadth, 2·6 mm. (increased by compression of seed).

REMARKS. A single seed similar to some awaiting description from the Lower Bagshot of Lake, differing chiefly in the absence of a deep apical emargination and of furrows both above and below the chalaza on the dorsal surface. Without a large range of material it is impossible to be sure that this is a constant and specific difference, moreover the Hengistbury seed is much compressed.

Family THEACEAE

Section TAONABEAE

In 1957 Chandler (p. 111) described from the Bovey Tracey Lignite of Devon three species of seeds with pitted testa and inverted U-shaped cavities under the name *Myrtospermum* a form-genus of the family Myrtaceae. *M. variabile* from the Bournemouth Freshwater Beds (V.34248) was cited as the type species (1957 : 112). Recently Professor P. I. Dorofeev in a personal communication has very kindly called attention to the resemblance between these supposed Myrtaceae seeds and the pitted seeds of *Eurya*, Theaceae, a family of which he had been making a study. Accordingly the detailed anatomy of herbarium material of the Theaceae was examined, the material being supplied by the courtesy of the Director of the Royal Botanic Gardens, Kew. The seeds available show that there is a closer correspondence between the fossils and seeds of certain genera of Taonabeae than exists in the seeds of Myrtaceae. These genera in addition to the characteristic coarse surface pits (which may appear as convexities if an outer thin epidermis is preserved) also show layers of small equiaxial cells inside the pitted surface. The number of these layers varies in different genera or species and may also vary in different parts of the seed in some species. The absence of this coat had been noted in studying the more comparable Myrtaceae such as *M. beckleri* and *M. viellardii* which had been compared with the fossils on account of their inverted U-shaped cavities and coarse-celled testa. Again the condylar cavity between the two limbs of the seed in Taonabeae is more sharply defined and agrees exactly in form and structure with that of the fossils.

The study of the Recent material available for dissection suggests that the limits of the genera in the Taonabeae are not always clear in the seeds although a larger range of material might demonstrate true generic differences. Thus *Eurya japonica*

Thunb. (R. D. Oldham, No. 92, Nagasaki) showed only a slight bent cavity which was comparable with that of *Adinandra dumosa* Jack (Botanic Gardens, Singapore, S.F.N. 24975). *Eurya japonica* var. *nitida* Dyer (W. Borneo, Pontianak Mondi, 267) showed a hooked cavity with the micropylar limb at least twice as long as the chalazal. In *Cleyera* sp. (El Salvador. J. M. Tucker, 653) the inverted U-shaped cavity agreed exactly with the fossil, the micropylar limb being only slightly longer than the chalazal and the condyle identical in its form and structure. Whether all species of *Cleyera* are constant in these respects could not be ascertained and the fossils can therefore be referred tentatively only to the genus but definitely to the section Taonabeae. The pitting of the surface in the species of *Eurya* and *Adinandra* seen was relatively coarser and as it followed the curvature of the bent or hooked cavities did not correspond so closely with the fossil as did that of *Cleyera*.

The species to be transferred from Myrtaceae to Taonabeae and provisionally to *Cleyera* (which is treated by Engler as a sub-genus of *Eurya*) are as follows : *Myrtospermum variabile*, *M. boveyanum*, *M. dubium* and *Myrtospermum* sp. (Chandler, 1957 : 112–113, pl. 16, figs. 160–174) and the following in Chandler (1960) *M. variabile* (p. 80, pl. 8, figs. 8, 9 ; p. 108, pl. 11, fig. 18 ; p. 335, pl. 34, figs. 16–18). *M. warreni* (p. 81, pl. 8, figs. 10, 11) and possibly Genus? (p. 81, pl. 8, figs. 12, 13). *M. cooperi* (p. 106, pl. 11, figs. 13–17). *Myrtospermum* sp. (p. 335, pl. 34, fig. 19). *Myrtospermum* sp. (p. 336, pl. 34, fig. 20). (*Myrtospermum* sp. (p. 108, pl. 11, figs. 19, 20) apparently does not belong to Taonabeae.)

The position of the genus *Palaeorhodomyrtus* (Reid & Chandler, 1933 : 436, pl. 23, figs. 21–31) calls for further examination in the light of these studies as does that of *Hightea* (Reid & Chandler, 1933 : 439).

Genus ***CLEYERA*** DC.

The seeds under discussion above occur in many English Tertiary deposits. Their outline approximates to circular, oval or triangular, they are somewhat flattened or lenticular. They split marginally into symmetric valves. Within is an inverted U-shaped cavity the limbs which are separated by a condyle, being slightly unequal. The large hilum is marginal at the end of the condyle, the chalaza is close to the hilum, terminal or sub-terminal on the inner side of the shorter broader limb ; the raphe lies in the thickness of the condyle between the limbs, it is recurved and folded upon itself in its passage to the chalaza. The micropyle is marginal adjacent to the hilum and terminal on the longer limb. The testa is hard, in the majority of species at least two or three layers of compact parenchyma surround the seed-cavity. They are succeeded, sometimes abruptly, sometimes gradually, by one or more layers of large prismatic cells radially or obliquely aligned with reference to the seed-cavity. In some specimens these large cells appear simple, in others they are obviously formed of fine parenchyma, a structure revealed more clearly by decay and abrasion.

Cleyera **?*variabilis*** (Chandler)

(Pl. 31, figs. 48–56)

1957. *Myrtospermum variabile* Chandler; p. 112.
1960. *Myrtospermum variabile* Chandler, pp. 80, 108, 335, pl. 8, figs. 8, 9; pl. 11, fig. 18; pl. 34, figs. 16–18.

About a dozen seeds from several horizons at Hengistbury have been compared with specimens from the Bournemouth Freshwater Beds and the Highcliff Sands, Cliff End, near Mudeford. There can be no doubt as to their identity. One somewhat distorted seed shows the curved limbs and U-shaped form particularly clearly (Pl. 31, fig. 54). This and several other specimens show the external pits separated by rounded ridges. Along the middle of the ridges are grooves indicating planes of weakness. This particular character is not usually apparent in seeds from other horizons but can be seen after careful scrutiny in a few specimens. As in the more typically abraded specimens from Cliff End and Sandbanks the pits and ridges of the Hengistbury seeds are built up of small rectangular cells.

Family THYMELIACEAE

Genus ***DAPHNE*** Linnaeus

Daphne sp.

(Pl. 31, figs. 46, 47)

DESCRIPTION. *Seed*: Obovoid, probably originally tapering to the pointed hilum, but the original form is doubtful as the hilar end is burst and broken. Probably anatropous (by analogy with living forms) more or less symmetrical. Testa and raphe abraded. Micropyle (by analogy with living) at the broken end. Chalaza at the rounded end indicated by a small aperture, 0·1 × 0·125 mm. in diameter, marking the point of entry of the raphe. Tegmen thick, about 0·1 mm. in transverse section but thinner towards the micropylar end, hard, brittle (as suggested by the cracking which has occurred). It is preserved in dull surfaced amorphous pyrites mud. External surface of equiaxial cells 0·025–0·03 mm. in diameter, but abraded so that at the angles between adjacent cells tiny apertures are exposed giving the whole surface an evenly pitted appearance the walls themselves being obscure. There are no large scattered depressions. In section the wall is formed of slightly curved columns, the curvature being convex towards the micropyle. Their inner ends produce polygonal shining slightly convex cells on the inner surface of the tegmen somewhat smaller than the cells on the outer surface. Length of seed (burst and imperfect at the hilar end), 2·25 mm.; maximum diameter, 1·75 mm.

REMARKS. One poorly-preserved seed now completely disintegrated. It closely resembled a seed of *Daphne* from the Lignite above the Boscombe Sands at Southbourne. In the broken state of the specimen it was impossible to be sure whether it ever possessed a comparable elongate-pointed hilar end. The slight tumescence which occurs over the chalaza of the Southbourne seed has not been seen, moreover the pits on its surface mark the cell cavities not the angles of the cells as in the Hengistbury fossil. These differences may, however, be the result of different degrees of abrasion rather than specific characteristics.

Family EPACRIDACEAE

Small subglobular five-loculed loculicidal fruits with solitary pendulous seeds occur in the Bournemouth Marine Beds, the Highcliff Sands and the Lower Headon of Hordle. Their general anatomy and cell-structure suggest that they belong to Epacridaceae. One poor specimen only has been found at Hengistbury.

Drude (1891) divides Epacridaceae into three sections: the Prionoteae and Epacrideae each with loculicidal capsules having several- to many-seeded locules, and the Stypheliae with solitary pendulous seeds in four-, five-, or ten-loculed fruits. Drude states that in this third section the hard bony syncarpous fruits are not loculicidal and are generally indehiscent. Some means of egress for the germinating seed must however have existed, and it is possible that prolonged maceration (as in fossilization) would reveal loculicidal planes of weakness not apparent in normally ripened fruits. It is probable therefore that the fossil species belong to the section Stypheliae with its single-seeded locules and pendulous seeds. In the absence of fuller information the fruits are referred to a form-genus *Epacridicarpum.*

Genus ***EPACRIDICARPUM*** nov.

Diagnosis. A form-genus for fruits referable to Epacridaceae of which the nearer relationship is not known.

Epacridicarpum mudense n. sp.

(Pl. 31, fig. 57)

Diagnosis. Fruits five-loculed, suboblate-sphaeroidal five-angled capsules, the angles overlying the locules, axis fibrous. External surface rough with elongate rugosities. Seeds solitary. Length of capsule, 1–1·1 mm.; transverse diameter, 1·2–1·45 mm.

Holotype. Brit. Mus. (N.H.), No. V.36486 from the Highcliff Sands, Cliff End near Mudeford, Hampshire, awaiting publication.

Description. Part of a five-loculed oblate-sphaeroidal capsule appears to be comparable with *Epacridicarpum mudense* now known from Hordle and Cliff End, Mudeford. This better material awaits publication. The Hengistbury specimen shows only two carpels, still united with loculicidal dehiscence. The external surface has shallow depressions over the septa producing slight wing-like projections over the locules. The external surface is somewhat rough, formed of equiaxial cells giving an unevenly pitted appearance. Locule lining shining, formed of long narrow cells (0·009 mm. broad) which diverge from the apical placentae situated at the inner angles of the locules. The remains of a placenta? (or shrivelled seed?) can be seen in one locule. Length of capsule, 1 mm.; breadth across the two united carpels, 1·1 mm. Maximum radius from axis to external surface, 0·75 mm.

Family CORNACEAE

Section MASTIXIOIDEAE

Genus ***MASTIXICARPUM*** Chandler, 1926 : 35

Mastixicarpum crassum Chandler

1926. *Mastixicarpum crassum* Chandler, p. 36, pl. 6, fig. 5, text-fig. 18.

The specimen was found in an ironstone concretion full of lignitic fragments. It is to be figured in a forthcoming monograph on the Lower Bagshot for convenience of comparison with material from other localities.

It shows the typical large germination valve extending throughout the length and occupying about one-quarter of the circumference. The median infold on the valve and the U-shaped locule are seen where the specimen is transversely fractured. The plane of weakness down the middle of the infold and the sutures which delimit the valve are visible and the radially arranged fibres of the wall. Length of endocarp, 9·75 mm.; maximum transverse diameter, 5·5 mm.

Family SYMPLOCACEAE

Genus ***SYMPLOCOS*** Jacquin

Symplocos sp. (?***Symplocos headonensis*** Chandler)

(Pl. 31, figs. 58, 59)

DESCRIPTION. *Endocarp*: Woody, subovoid (somewhat flattened in fossilization), truncated at the apex by a depression originally occupied by the perianth disc which has disappeared. Four-loculed, with the four apical apertures opening into the apical depression. Apertures and locules unequally developed. Basal scar of attachment marked by a small depression displaced owing to the distortion of the endocarp. Seeds project from two of the locules (they have been partially squeezed out by pressure in fossilization), two were visible in one locule and one in another. Surface of endocarp smooth, structure obscure. Surface of seeds formed by elongate cells arranged in rather irregular and sinuous groups. Length and breadth of endocarp, 5·5 mm. (as laterally compressed). Greatest diameter across the apical depression, 2 mm.

REMARKS. In spite of its poor condition the characters are unmistakably those of *Symplocos*. It probably belongs to *Symplocos headonensis* Chandler (1926 : 40) a form common at Hordle, present also at Sandbanks (Bournemouth Freshwater Beds) and Arne (Lower Bagshot).

Family ?

Genus ***RHAMNOSPERMUM*** Chandler, 1925 : 30

Rhamnospermum bilobatum Chandler

(Pl. 32, figs. 60, 61)

1925. *Rhamnospermum bilobatum* Chandler, p. 30, text-fig. 13.
1926. *Rhamnospermum bilobatum* Chandler : Chandler, pl. 5, fig. 1*a–c*.
1926. *Rhamnospermum bilobatum* Chandler : Reid & Chandler, p. 117, pl. 8, figs. 1, 2.

Specimens are of common occurrence. They show the characteristic bilobed form and polygonal cells. Most are so abraded that the shining inner coat is exposed wholly or in part. Many have been flattened in fossilization but a few show the typical inflated form. The true systematic position of this problematical " seed " is still obscure. It is now known from many horizons and is fully described and discussed in a mongraph of the Lower Bagshot flora awaiting publication. The size of the species, if indeed it is a true species, is very variable. The Hengistbury material only varies in length from 2 to 2·2 mm. The breadth across the lobes which are flattened one upon the other is 1·2–1·5 mm. The surface cells are about 0·018–0·027 mm. in diameter.

In the dark basal sands at the west end of the Headland several seeds (V.36415, V.36416) were found and were so abraded that only an inner integument was preserved. A much battered seed was also found 40 ft. above the basal pebble bed in the Upper Hengistbury Beds (V.36414). Some specimens are from 25 ft. above the pebble bed (V.36411, V.36412).

INCERTAE SEDIS

Carpolithus cornutus n. sp.

(Pl. 32, figs. 62–66)

DIAGNOSIS. *Fruit* : One-loculed, approximately bisymmetric with a median longitudinal angle in the plane of symmetry, splitting along the angle into subequal valves. Base prominent, apex projecting, pointed. Each valve bears 5 or 6 solid large pointed horns or spines in the upper two-thirds (? tips of a persistent perianth). Length of fruits about 4·5–5 mm. ; breadth, 4·75–5·5 mm.

HOLOTYPE. Brit. Mus. (N.H.), No. V.36417.

DESCRIPTION. The species is represented by two mature fruits and at least one, perhaps two, immature specimens. Mature fruits are one-loculed, more or less bisymmetric with a projecting horn-like apex which is longitudinally angled in the plane of symmetry. The fruits split along the angle into two more or less equal valves. There is a prominent basal attachment 1 mm. broad, and a projecting pointed horn-like apex. Each valve bears several spines in the upper two-thirds, 6 were counted on one valve of a mature fruit, fewer (but some were broken) on the other valve. The pyritized wall is seen in section in the broken spines. Below the spines the fruit wall is smooth and longitudinally striate due to longitudinally aligned and elongate cells about 0·027 mm. broad. Much of the surface is obscure owing to sand pitting but near the tip of one spine small inflated oblong cells can be seen parallel to the length of the spine.

Locule walls compact and lignified (cell-structure obscure) 0·114–0·17 mm. thick. Outside the compact wall there is a thicker but looser textured coat of which the cells lie parallel with the surface of the fruit when the coat is seen in section. Locule lining striate, the striations and cells which produce them diverging from the attachment and longitudinally aligned. The alignment indicates an organ at each end of the fruit. When best preserved the cells are seen to be rectangular, 0·027 broad, black and shining, very slightly toothed. The horn-like spines appear to be formed from the outer coat; they are solid in section and show no sign of a cavity. Sometimes the outer coat peels off from the surface of the fruit leaving exposed a smooth endocarp destitute of spines which have come off with the outer coat (? exocarp). Examination of an immature fruit suggests that the horns and outer coat may be produced by a persistent perianth and bracts for in this specimen they do not appear to be completely fused to form an integument (Pl. 32, fig. 65). Length of one fruit from basal attachment to tip of apical spine, 4·5 mm.; breadth, 5·5 mm. (tip of one spine incomplete). Length of a second specimen, 5 mm.; breadth, 4·75 mm. (one spine slightly imperfect at the tip). Length of immature specimen, 2·5 mm.; breadth, 3·25 mm.

REMARKS. Three specimens described above and a fourth doubtful immature specimen. All are somewhat distorted by compression parallel to the plane of approximate symmetry. In the immature fruit (if the same) the individuality of the bracts or perianth segments which form the horns is clearly shown.

It is tempting to connect these horned fruits with *Trapa* but the superficial likeness is dispelled by careful comparison. In *Trapa* there are always four conspicuous horns. There may be subsidiary horns borne on the main ones as in specimens from Reuver making as many as eight in all. The apical " crown " (style base) is a conspicuous feature.

There is some resemblance in the one-loculed endocarp with solitary (? basal) seed to Juglandaceae but none of this family has the conspicuous horn-like processes, nor the close-textured compact endocarp. There is no trace of basal lobing as in Juglandaceae.

The relationship has not been discovered.

Carpolithus sp.

(Pl. 32, figs. 67, 68)

A small pyritized flattened fruit 2 mm. long, 2·2 mm. broad at the apex is subtriangular in outline with convex apex, slightly concave sides and rounded narrowed base. It thickens towards the broad apical end where a series of bracts free at their tips are fused to form the fruit below. There is one projecting fruit or pointed bract with three angles or ridges. Four fused bracts lie on one side of it and two which partially embrace it on the other. On the flat broad surface of the fruit there are three longitudinal ribs alternating with four furrows on one side (that which terminates in four bracts) while on the other side there is one median furrow. The specimen appears to be surrounded by a thin perianth.

Its general appearance recalls a bract of *Alnus* female cone but the structure does not correspond in detail. Moreover the base is smoothly finished not ragged or truncated like the base of an alder scale which has been torn from the cone. It may be a small fruit, perhaps immature, rather than a cone-scale.

Carpolithus sp.

(Pl. 32, fig. 69)

A tiny apical (?) fragment of the valve of a woody endocarp. The external surface has a flat rim 0·3–0·5 mm. broad. Within the rim is a coarse network of ribs. Inner surface more or less smooth. Apex (?) somewhat pointed. Maximum length and breadth of fragment about 2·5 mm.

Carpolithus sp.

(Pl. 32, figs. 70, 71)

Several fragments of a smooth-walled thin woody endocarp. One specimen is somewhat flattened and has a truncate end (apex ?) (Pl. 32, fig. 70), rounded base with slight rim round side and base delimited by a shallow groove from the median flat broad area. Length about 2·5 mm. ; breadth, 2·25 mm.

The specimen has broken and shows two locules lying side by side within the breadth of the specimen. A pair of apertures at the truncate end lead into the two locules. External surface with scattered dimples or depressions. Wall in section lignified and shining, structure obscure but fine-celled. Internal surface encrusted with pyrites so that the cell-structure is hidden.

A fragment of a second specimen (V.36424) shows in addition to the irregular dimples small equiaxial cells, 0·023 mm. in diameter. Another fragment (Pl. 32, fig. 71) may also belong to the same species from its surface characters.

Carpolithus sp.

(Pl. 32, fig. 72)

A shining semi-translucent lining layer of a crushed elongate suboval fruit shows three small blunt stylar prominences at the narrower end. The broader end is truncated by a large aperture which may mark the site of a scar of attachment now torn away as the margin here is thin and slightly irregular. Whereas the specimen was probably originally inflated it is now collapsed and crumpled. Within some of the folds remains of a rough thicker outer carbonaceous coat can be seen but its structure is obscure. Surface of the shining coat formed of rounded more or less equiaxial cells at least 0·057 mm. in diameter, sometimes instead of being strictly equiaxial there is a tendency for these cells to be slightly transversely elongate. There are also indications of an inner (?) layer of transversely elongate narrow cells. Length of fruit including style, 1·8 mm. ; breadth, 0·75 mm.

In the absence of more abundant material and better evidence, no attempt is made to determine the specimen although certain features such as the three styles and the cell-structure suggest Cyperaceae. The specimen would certainly be recognizable again.

11. *Plant Remains from the Bartonian of Barton Cliffs (Horizons A1 to L of Burton, 1933), Hampshire*

GYMNOSPERMAE

Order CONIFERALES

Family ARAUCARINEAE

Genus ***ARAUCARITES*** Presl

? ***Araucarites sternbergi*** Goeppert

See p. 201.

A small twig fragment about 36 mm. long, with slender falcate leaves was figured by Gardner, referred doubtfully to this species, and alluded to on p. 59 of his account of *Araucaria goepperti* from the Bournemouth Freshwater and Marine Beds (1883 : 55–59). The fragment came from the " Middle Bagshot of Highcliff " at Barton (= Lower Bartonian) and was in the British Museum collection. In the absence of further evidence its specific identity must be regarded as doubtful but its appearance strongly suggests *Araucarites*. It is unlikely that Gardner who knew the genus well at Bournemouth would have been mistaken. He refers elsewhere (1887 : 249) to " branches of apparently the Bournemouth *Araucaria* " in the Highcliff Beds. Reasons for referring it to the species *Araucarites sternbergi* are given on p. 201.

Family ABIETINEAE

Genus ***PINUS*** Linnaeus

Pinus sp. (? ***Pinus bowerbanki*** (Carruthers))

(Pl. 32, figs. 73, 74)

1850. ? *Pinites dixoni* Bowerbank (pars) *in* Dixon, p. 84, pl. 9, fig. 4.
1878. ? *Pinites bowerbankii* Carruthers *in* Dixon, p. 163.
1884. *Pinus bowerbankii* (Carruthers) Gardner, pp. 68, 69, pl. 13, figs. 6, 9.

DESCRIPTION. *Cone* : Elongate-ovoid, about 8·5 cm. long as preserved, but imperfect at both base and apex, much compressed laterally, about 4·1 × 2 cm.

in transverse diameter. About forty scales appear to be still attached, but are difficult to count owing to the decayed condition of some of them. They show rhomboidal apophyses, the largest being about 17 mm. broad and 10 mm. deep, having a prolonged slightly recurved dorsal umbo and a marked transverse carina ; below the carina the apophyses are ornamented with divergent striae. The specimen was rapidly disintegrating at the time of its discovery in 1938. It differs from a cone ascribed to *P. dixoni* (Bowerbank) Gardner (1884) in the larger more sharply carinate apophyses (Pl. 33, figs. 75–79). It also differs in exactly the same way from somewhat similar cones of *P. dixoni* from Hengistbury (p. 202, Pl. 29, figs. 12, 13 ; Pl. 30, figs. 14,15). Probably therefore it must be regarded as distinct from *P. dixoni*. It must, however, be remembered that living pines show considerable variation both in size of cone and in the size of apophyses in a single species ; also, that the fossils are in a poor condition which adds to the difficulty of determination. A second cone (V.32596) now rapidly decaying was found by F. C. Stinton at Horizon C.

The characters described and figured above suggest relationship with a cone collected by Gardner at Bracklesham and figured by him as *P. bowerbankii* (Carruthers) (1884 : 68, pl. 13, fig. 9). In his account of this cone he stated that the type of *P. bowerbanki* was no longer extant and that this ill-defined species was based by Carruthers on mutilated and possibly incorrectly described material. He concluded, therefore, that whereas the resemblance between cones he had himself examined from Bracklesham, Sheppey and Highcliff (1884, pl. 13, figs. 6, 9 ; pl. 14, figs. 3, 8) was such as to place them, in his opinion, in a single species, the relationship of this species to Carruthers' original *P. bowerbanki* must remain doubtful.

According to Keeping (quoted in Gardner, 1884 : 69) cones of *P. bowerbanki* have occasionally been abundant at Highcliff.

It may be noted, that Reid & Chandler transferred Sheppey cones referred by Gardner to *P. bowerbanki* to *Pityostrobus* sp. (1933 : 94) but that further consideration of the matter necessitates a return to the original ascription to *Pinus* (Chandler, 1960 : 120).

Pinus sp. (? ***Pinus dixoni*** (Bowerbank))

(Pl. 33, figs. 75–79)

1884. *Pinus dixoni* (Bowerbank) : Gardner, p. 66, pl. 13, figs. 1–5, 8 ; text-fig. 27 on p. 67.
1933. *Pityostrobus dixoni* (Bowerbank) : Burton, p. 151.

An elongate-ovoid cone was found by E. St John Burton in a dark, rather sandy and gritty clay at Horizon D (cf. Burton, 1933 : 142, 151). The cone was 11·6 cm. long, 3·9 cm. broad but was much compressed so that in life it must have been somewhat narrower. Unfortunately it fell to pieces immediately as commonly happens with such cones but not before Burton had made a rough sketch of it. A few of the scales were figured and sent to Prof. R. Florin of Stockholm for examination. He reported (23.x.35) that the material sent was too fragmentary and badly preserved to justify exact determination. The determination of isolated pine-cones, he stated, must be based on a study of the apophyses. In the case in question, however, only a few detached scales could be sent to him and these were badly compressed and probably considerably altered in appearance. Moreover there was no indication as to what part of the cone they came from while scales often look somewhat different at the ends of a cone.

He concluded, " However, I think there can be no doubt that the cone with its large number of scales belongs to the sub-genus *Diploxylon*. It seems probable that it resembled more or less the cones of certain Recent species belonging to the groups *Lariciones* and *Australes* of G. R. Shaw (1914). The apophyses seem to have been rhomboidal, or, according to the drawing irregularly pentagonal in outline and they possess a dorsal prolonged umbo and a transverse carina.

" In the dimensions of the cone . . . as well as in the structure of the apophysis the Barton cone resembles *Pinus dixoni* (Bowerb.) Gardner ... This species is of course not very well defined as being based on an imperfectly preserved material. But I doubt if there is much more to be done than to refer it, with or without query to *Pinus dixoni*, hoping that some day a more satisfying material will be found."

The discovery of well-preserved *P. dixoni* at the top of the Lower Hengistbury Beds at Hengistbury Head (p. 202, Pl. 29, figs. 12, 13 ; Pl. 30, figs. 14, 15) lends support to the provisional determination of the poorly-preserved Barton clay specimen more especially as *Nummulites prestwichianus* (a Barton species) has been found by D. Curry a few feet above in the Upper Hengistbury Beds (i.e. 15 ft. above the basal pebble bed of the Hengistbury Series) (see Curry, 1942).

In a letter dated 29th October, 1935, Burton reported that he had formerly obtained another similar cone in the Lower Barton Beds (A1) (cf. Burton, 1933 : 135, 151) and that the species could also be collected from the Middle Bartonian (Horizon E). He also listed the same species at Horizons A3, A1, E, ?H (1933 : 151).

Family TAXODINEAE

Genus ***SEQUOIA*** Endlicher

Sequoia couttsiae Heer

(Pl. 33, figs. 80, 81)

See p. 204.

Twigs obviously referable to *Sequoia couttsiae* Heer, a species abundant in beds above and below occur at various horizons in the Barton Beds. They are not very common and are usually encrusted with pyrites (Burton, 1933 : 137, 142, 151). In the Lower Bartonian at Horizon A3, the Middle Bartonian (Horizon D) and the Upper Bartonian (Horizon L), specimens in better condition have recently been obtained. Even so, the condition does not lend itself to cuticle preparation, and the specimens are very liable to decay completely. Burton lists *Sequoia* sp. at Horizons A3 and D (1933 : 151).

CONIFERAE

Family ?

Genus ?

(Pl. 33, figs. 82, 83)

Two minute twig tips with short broad imbricate scale-like curved leaves with fringed margins recall the young twigs found in the Bournemouth Marine Beds awaiting publication (as *Cupressistrobus gardneri* Chandler ; see also Chandler, 1960 : 62, 112). Without more and better preserved material it is impossible to make a satisfactory determination.

ANGIOSPERMAE

Class MONOCOTYLEDONES

Family POTAMOGETONACEAE

Genus ***LIMNOCARPUS*** C. Reid emend. Reid & Chandler, 1926 : 68

Limnocarpus headonensis (Gardner)

(Pl. 33, figs. 84–86)

See p. 205.

Two subovoid locule-casts of *Limnocarpus* evidently belong by their size and proportions to *L. headonensis* although in the absence of the endocarp itself evidence of the external rugosities is not preserved. The curved form of the carpel is clear with large rounded lobe below and smaller one above, the two being separated by a long oblique groove (cast of condyle) on each broad surface. In one specimen the cast of the keel (or germination valve) is preserved. It is sub-triangular in outline, rounded below, pointed above, not reaching the style with a conspicuous median longitudinal ridge and less marked marginal longitudinal ridges. Abraded indications of style and stalk can be seen in one specimen only. Length of endocarp about 1·75 mm. ; breadth in plane of symmetry, 1·2 mm. ; thickness, 1·2 mm.

Family HYDROCHARITACEAE

Genus ***STRATIOTES*** Linnaeus

Stratiotes hantonensis Chandler

(Pl. 33, figs. 87–95)

See p. 205.

Typical seeds of the species were found in a very water-worn condition so that their longitudinal ridges were much obliterated. Some were suboval in outline with projecting rounded " collar ", others sigmoidal. Seeds inflated with more or less clearly differentiated flattened narrow keel merging into the collar or terminating against it. Collar smooth, marked off by a constriction from the body of the seed. Testa woody coarsely pitted (the pits about 0·05 mm. in diameter). Pits are more or less longitudinally elongate and aligned. Micropyle basal or sub-basal, sometimes traversing the collar obliquely. Hilum on the keeled margin variable in position, at the extremity of the hook at the chalazal end in sigmoidal seeds, towards the base or half-way along the margin in hooked seeds. Raphe marginal to the apex in hooked seeds then passing directly across the keel to the apical chalaza. Possibly abraded along the margin in sigmoidal seeds remaining only as a short transverse canal across the upper end of the keel. Digitate cells of interior of keel longitudinally aligned, occasionally slightly sinuous. The seeds (allowing for their more worn condition) are identical with specimens from Southbourne, Hengistbury and the Highcliff Sands, Cliff End, Mudeford. Some are small examples but equally small or smaller ones occur at Southbourne. Length of seeds, 3 mm.; breadth, 1·5–1·6 mm. A fragment (not measured) shows a somewhat broader seed. Seeds are from Horizons A2, A3 (V.36431–36435) and there are a few seeds collected by H. Eliot Walton, labelled " Bartonian " (V.36436).

Stratiotes headonensis Chandler

(Pl. 33, figs. 96, 97)

1923. *Stratiotes headonensis* Chandler, p. 125, pl. 5, figs. 1–3, 24–26; pl. 6, fig. 23.
1925. *Stratiotes headonensis* Chandler: Chandler, p. 14.

A valve of a seed (incomplete at the micropylar end) shows the typical flat keel with highly contorted cells on its inner surface, also the long marginal raphe, and marked longitudinal ribs of *S. headonensis*. It has been compared with specimens from Hordle and there can be no doubt as to its specific identity.

Family CYPERACEAE

Genus ***CARICOIDEA*** Chandler, 1957 : 86

Caricoidea obscura Chandler

(Pl. 33, figs. 98–105)

See p. 207.

A number of fruits and endocarps which cannot be distinguished by their structure from typical specimens of *Caricoidea obscura* from Highcliff Sands, Cliff End, Mudeford (see p. 207) although they tend to be somewhat larger. Length of fruit, 2·3 mm.; breadth, 1·75 mm. Length of another specimen, 2 mm.; breadth, 1·5 mm. The fruit in fig. 99 shows at the apex a three-rayed ridge perhaps originally associated with three styles. That in fig. 100 appears to have been larger and broader when perfect, the mucronate endocarp is partly obscured by remains of fruit in the lower half. It should possibly be regarded as distinct, but on the other hand the different appearance may be due to differential abrasion. The length and breadth, as preserved, are 1·5 mm.

The Barton endocarps are similar to typical *C. obscura* in their external surface. Some have a markedly conspicuous mucro. Some contract gradually to the basal neck while in others the neck is more distinctly defined (Pl. 33, figs. 102–104) but there appear to be no grounds for separation into more than one species. Length of an endocarp, 1·25 mm. ; breadth, 1 mm. Length of another, 1·25 mm. ; breadth, 0·9 mm.

Class DICOTYLEDONES

Family NYMPHAEACEAE

Genus ***BRASENIA*** Schreber

Brasenia ovula (Brongniart)

(Pl. 33, figs. 106, 107)

See p. 210.

The seeds have been often described and are too familiar to need more than a record here.

Fragments too incomplete to be worth illustrating but showing typical digitate cells aligned in longitudinal rows have been obtained by D. Curry at Horizon A3. Abrasion sometimes produces the effect of equiaxial cells at the surface, about 0·016 mm. in diameter. Seeds are also common in Beds K and L (V.36446–36449).

Family CAPPARIDACEAE or THEACEAE?

Genus ?

(Pl. 33, figs. 108, 109)

DESCRIPTION. *Seed* : Subcircular in outline, somewhat reniform owing to a marked emargination at the hilum, bisymmetric, probably splitting marginally for germination in the plane of symmetry, but one valve is largely destroyed. Cavity inverted U-shaped, the " U " formed by the inner integument (tegmen), now much decayed. Limbs very unequal, the micropylar limb considerably longer than the other which is broader. Both limbs rounded at the extremities. Axis between limbs oblique to the straight side of the semicircular outline. Internally there is a short condyle between the limbs, externally there is a broad thick funicle. Seed when perfect much inflated. Testa deeply foveolate externally, the large pits about 0·05 × 0·025 mm. in diameter superficially are seen in section to occupy about one-third of the thickness. These pits are aligned parallel with the outline of the seed and are elongate radially. They become very small towards the centre of the seed and at the tips of the two limbs. Structure of the inner part of testa obscure but apparently formed of several rows of small square cells about 0·01 mm. in diameter. Lining of seed-cavity of long narrow cells which diverge from the condyle crossing the limbs transverse to their length. Maximum diameter of seed about 1·75 mm. (estimated, slightly imperfect) ; breadth measured across the two limbs, 1·4 mm.

REMARKS. One imperfect seed shows the characteristic form and surface of certain Capparidaceae or Theaceae. Form and ornamentation combined with size appear distinctive but the specimen is now badly decayed so that no name has been given.

Family ANONACEAE

Genus ***ANONASPERMUM*** Ball emend. Reid & Chandler, 1933 : 184

Anonaspermum sp.

(Pl. 34, figs. 110–113)

DESCRIPTION. *Seed*: Subovoid, somewhat compressed, bisymmetric, ruminate, the ruminations coarse varying in thickness and length, irregularly transverse over the middle of the seed and diverging at one end (probably at both but only one exposed), anastomozing, branching and bifurcating near the margin, sometimes continued from side to side, sometimes interrupted over the middle ; cells decayed. Length of seed, 9 mm. ; breadth, 7 mm.

REMARKS AND AFFINITIES. One seed collected by H. Eliot Walton. It is broken in half along the plane of symmetry through the marginal raphe and chalaza. Both halves are now incomplete. One half retains the testa much decayed and coated with pyrites. The character of the ruminations makes the relationship with Anonaceae clear. As stated by Reid & Chandler (1933 : 182) the generic and specific characters are not well defined in the seeds of this family hence the fossil must be referred to the form-genus *Anonaspermum*. In size, shape and character of the ruminations it resembles *Anonaspermum rugosum* Reid & Chandler (1933 : 186, pl. 5, figs. 21–24) from the London Clay, but it lacks the depressed central area of that species. It is said to come from the Barton Beds and is definitely from the Hampshire coast section between Highcliff and Hordle Cliff.

Family RUTACEAE

Genus ***RUTASPERMUM*** Chandler, 1957 : 102

Rutaspermum sp.

(Pl. 34, figs. 114, 115)

DESCRIPTION. *Seed*: Gibbous in outline, not markedly inflated, not beaked at the apex. Ventral margin straight, occupied in the upper part by the elongate-triangular shallow hilar depression which extends from the apex for about two-thirds of the length of the seed. Surface ornamented with finely sinuous longitudinal ribs which may branch and anastomoze occasionally and are sometimes connected by short transverse branches ; formed of equiaxial or elongate pits about 0·027 mm. in diameter. Testa thick ; area surrounding hilar depression not quite so rugose as the broad surfaces. Length of seed, 6 mm. ; breadth, 3·75 mm. ; thickness, 2·5 mm.

REMARKS. One seed which somewhat resembles *Zanthoxylon ornatum* Chandler from the Lower Headon of Hordle in size and ornamentation but it is less beaked on the ventral margin and is not so very conspicuously smooth around the hilar scar as is that species. The latter difference may be due to the greater abrasion of the Hordle fossils but is a constant feature of them. It therefore appears advisable to refer the Barton fossil merely to *Rutaspermum* sp. until more material is available.

Rutaspermum sp.

(Pl. 34, figs. 116, 117)

Description. *Seed* : Half-anatropous, approximately bisymmetric about a plane including the hilar scar, raphe, and chalaza, inflated, sub-triangular in outline with rounded angles, having an almost straight faceted ventral margin and gibbous dorsal margin ; lateral faces smoothly convex, meeting along the dorsal margin at a rounded angle of about 100°. On the ventral facet is the sunk elongate narrowly triangular hilar scar, 5 mm. long ; 1·5 mm. broad at the widest point. Raphe canal short, curved, entering the testa at the broad end of the hilar scar. The large black circular chalaza is situated at the rounded angle on the gibbous dorsal margin. A pair of depressions form a marginal constriction between this angle and the point where the raphe enters the testa (probably marking the ventral limit of the chalaza). Surface much decayed, smooth and shining in a few better preserved patches, ornamented with finely crenulate pits like those of the middle black integument in living *Zanthoxylon* seeds. Each pit is about 0·05 mm. in diameter. Length of seed in the plane of symmetry parallel with the ventral margin, 8 mm. ; diameter at right angles to the hilar scar in the plane of symmetry, 7 mm. ; diameter at right angles to the plane of symmetry, 6 mm. ; thickness of testa where exposed, 0·5 mm.

Remarks and affinities. One seed collected by H. Eliot Walton at Barton (precise locality unknown). Characters of form, hilum, raphe, chalaza and sculpture are those of Zanthoxyleae. No comparable living genus has been recognized. Seeds of species of *Zanthoxylon* bear some resemblance to the fossil but are so much smaller as to exclude the fossil from the genus. Also the symmetrical lateral depressions appear to be without parallel among living genera. No specific name has been given and the seed has now disintegrated.

Family Icacinaceae

Genus ***ICACINICARYA*** Reid & Chandler, 1933 : 344

Icacinicarya pygmaea n. sp.

(Pl. 34, figs. 118–121)

Diagnosis. Endocarp gibbous in outline with slightly convex funicular margin having a rounded longitudinal ridge and gibbous opposite margin. Length, 1·4–1·5 mm. ; breadth, 1·5–1·75 mm. ; thickness, 1·1–1·4 mm.

Holotype. Pl. 34, fig. 119. Now decayed as is all the material but the characteristics are peculiarly distinctive.

Description. *Endocarp* : One-loculed, bisymmetric, with lateral funicle in the plane of symmetry. Funicular margin slightly convex, opposite margin gibbous hence the outline viewed at right angles to the plane of symmetry is roundly triangular or more or less gibbous. Inflated so as to be elliptical in transverse section and in sections at right angles to the plane of symmetry. Funicular margin having a marked longitudinal rounded ridge which narrows towards the basal attachment. It is flanked at the apex by a pair of small apertures or short canals. Style terminal between the apertures. Base broad and slightly flattened. External surface finely nodular or rugose with rounded rugosities which diverge from the style. External cell-structure equiaxial, cells about 0·025 mm. in diameter with finely toothed outlines. At the apex, inside, a large circular micropylar scar can be seen on adherent remains of the seed, 0·25 mm. in diameter. Cell-structure of interior decayed. Thickness of wall, 0·1 mm. Dimensions of several endocarps are: 1) Length (base to style), 1·5 mm.; breadth in plane of symmetry, 1·6 mm. Thickness at right angles to this, 1·25 mm. 2) Length, 1·5 mm.; breadth, 1·6 mm.; thickness, 1·3 mm. 3) Length, 1·4 mm.; breadth, 1·5 mm.; thickness, 1·25 mm. 4) Length, 1·5 mm.; breadth, 1·75 mm.; thickness, 1·4 mm. 5) Length, 1·5 mm.; breadth, 1·6 mm.; thickness, 1·1 mm.

REMARKS. Eight fruits and several fragments, of which five were perfect or almost so. The carpel wall was in all much pyritized and cracking. No such small endocarps have been seen either among living or fossil material. The smallest specimen previously recorded is *I. bognorensis* Reid & Chandler; length, 4 mm. (1933: 355, pl. 16, figs. 37, 38). The gibbous form is also a peculiar and distinctive feature.

Icacinicarya bartonensis n. sp.

(Pl. 34, fig. 122)

DIAGNOSIS. Endocarp bisymmetric, subglobular, with two apertures flanking the funicular canal at the apex. Length incomplete; transverse diameters, 2 × 1·75 mm.

HOLOTYPE. Brit. Mus. (N.H.), No. V.36452.

DESCRIPTION. *Endocarp*: Subglobular, bisymmetric, having a lateral canal for the funicle in the plane of symmetry flanked at the apex by a pair of small apertures (indicative of the small projecting horns with canals such as occur in *Iodes* and other genera). Surface much worn. Length of endocarp always incomplete (estimated length about 2 mm.): transverse diameter in plane of symmetry, 2 mm.; transverse diameter at right angles to plane of symmetry, 1·75 mm.

Seed: Represented only by traces of the testa formed of small square or polygonal cells about 0·01 mm. in diameter.

REMARKS AND AFFINITIES. The funicular canal and apical apertures in this bisymmetric endocarp place it in Icacinaceae and probably in the section Iodeae. The base is always incomplete but enough is preserved to show the form. The funicle is exposed by abrasion of the surface. The chief peculiarity is the small size combined with the subglobular form. It is larger than *I. pygmaea* and lacks the striking gibbous outline of that species. In addition to the holotype there are four other specimens all collected by A. G. Davis (V.36453).

Genus ? (? **Natsiatum eocenicum** Chandler)

(Pl. 34, fig. 123)

A fragment of one valve of a large inflated endocarp shows part of the margin. Surface ornamented with shallow concavities separated by well-defined ridges which form a network. On the locule-wall the external concavities are represented by slight convexities. External surface too abraded to show cell-structure. Locule surface also much worn with traces of what appear to be fine digitate cells. Possibly an inflated specimen of *Natsiatum eocenicum*. Maximum diameter of fragment, 6 mm.

Genus ***STIZOCARYA*** Reid & Chandler, 1933 : 336

Stizocarya sp.

(Pl. 34, fig. 124)

Description. *Endocarp* : Almost globular but obscurely bisymmetric, splitting in the plane of symmetry into equal valves. One-loculed, one-seeded, wall 1–1·2 mm. thick, formed of many layers of cells with tortuous or sinuous walls. The cells vary considerably in size and shape. The wall has a tendency to split irregularly into concentric layers, the outer layers being more compact than the inner. Locule lining formed of large digitate cells obscured by the state of preservation (shrinkage on drying having caused the inner surface to break up into small blocks). Carpel wall traversed by radially-directed cylindrical bundles of elongate cells like those which form the hair-bases in *Stizocarya communis* Reid & Chandler (1933 : 336, pl. 15, figs. 35–42 ; text-fig. 8). The bundles do not actually pierce the locule-wall but produce rounded low tumidities on its surface. On the external surface of the endocarp they give rise to circular scars about 0·15 mm. in diameter and about 0·4 or 0·5 mm. apart. Diameter of endocarp, 9·5 mm.

Seed : Represented by part of the thin papery testa and by its impression on a film of pyrites inside the locule. It is formed of angular equiaxial cells, about 0·03–0·05 mm. in diameter which are inflated externally ; a circular scar from which the cells diverge marks the chalaza.

Remarks and affinities. One much decayed endocarp from the Middle Bartonian of Barton cliff collected by W. Lennie Ames. While the evidence of the hair-bases clearly indicates *Stizocarya* the preservation of this single specimen is too poor to allow of specific determination although in size the endocarp is more or less comparable with *S. communis* (11–14·5 mm.).

Family Theaceae

Genus ***HORDWELLIA*** nov.

Diagnosis. Inferior three-loculed berries with axile placentation and numerous seeds in each locule. Seeds anatropous, bisymmetric, splitting in plane of symmetry which passes through raphe, hilum and micropyle. Testa much thickened between hilum and micropyle. Surface deeply and coarsely pitted, wall formed of small equiaxial cells. Length of seeds very variable, often about 1–1·5 mm.

TYPE SPECIES. *Hordwellia crassisperma* (Chandler).

Hordwellia crassisperma (Chandler)

(Pl. 34, figs. 140–144)

1926. *Actinidia crassisperma* Chandler, p. 34, pl. 6, fig. 2 ; text-fig. 15.

DIAGNOSIS. That of genus.

HOLOTYPE. Brit. Mus. (N.H.), No. V.20069 from Lower Headon of Hordle, Hampshire.

Anatropous pitted seeds described originally from Hordle but in far greater detail from the Lower Bagshot (awaiting publication). Fruits unknown in the Lower Headon have now been found at Bournemouth. At Barton there are anatropous pitted seeds showing all the characters described. The seeds vary in size and coarseness of pitting but there appear to be no adequate grounds for separating them into different species. The characteristic layers of small equiaxial cells form the inner part of the testa. One seed (Pl. 34, fig. 141) is crushed dorsiventrally so as to show the hilum facing the observer. Another (Pl. 34, fig. 140) is a typical small seed such as occurs abundantly in the Lower Headon of Hordle.

Although originally referred to *Actinidia* this relationship can no longer be maintained, for in *Actinidia* the coarse external cells are visible also on the inner surface of the testa, there being no inner layer of fine cells to conceal them. In *Hordwellia* the structure of the testa with its large external pits and inner compact layers of fine cells closely resembles that of seeds belonging to the Taonabeae and they are therefore referred to this section of Theaceae. As they do not agree with any living genus yet seen, the new generic name *Hordwellia* is given.

Dimensions of seeds : 1) Length, 1 mm. ; dorsiventral diameter, 1 mm. ; thickness, 0·75 mm. 2) Length, 1·5 mm. ; dorsiventral diameter, 1 mm. ; thickness, 0·75 mm. 3) Length, 1·15 mm. ; diameter, 0·75 mm. (This seed is dorsiventrally flattened.)

Genus ***CLEYERA*** DC.

Cleyera ? ***variabilis*** (Chandler)

(Pl. 34, fig. 145)

See p. 213.

DESCRIPTION. *Seed*: Truncated oval in outline, somewhat inflated, bisymmetric parallel with the broad surfaces. Cavity inverted U-shaped as indicated by impression of condyle between limbs seen on surface and by the alignment of the external pits. Hilum a large oval scar between the limbs on the truncate margin. Surface deeply pitted, pits arranged in concentric rows parallel with the margin, smaller over the central area (condyle) between the limbs than elsewhere. Internal structure not seen. Length of seed (measured along axis between limbs), 1·75 mm.; breadth (across two limbs), 1·5 mm.

REMARKS. A typical seed. For other remarks see pp. 212, 213.

Cleyera ? *bartonensis* n. sp.

(Pl. 35, figs. 151, 152)

DIAGNOSIS. Seed roundly triangular in outline, obliquely oriented so that the limbs lie parallel with two adjacent margins of the triangular outline, the hilum being close to the angle between these two margins. Dimensions of seed, 3·75 × 3 mm.

HOLOTYPE. Brit. Mus. (N.H.), No. V.36469.

DESCRIPTION. *Seed:* Bisymmetric, splitting in the plane of symmetry into equal valves for germination (one only preserved); much compressed at right angles to plane of symmetry, rounded-triangular in outline, hilum at one angle of the triangle. One limb of curved seed-cavity and the condyle which separates the limbs parallel with one of the sides of the triangle which arises from the hilar angle giving to the seed an oblique orientation parallel with its greatest diameter (Pl. 35, fig. 152). Limbs unequal, the micropylar limb the more slender and straighter of the two, the chalazal limb somewhat broader and markedly curved. Micropyle terminal on the slender limb, possibly large and gaping but the orifice somewhat obscure owing to a slight break in the testa. Chalaza terminal on the other limb connected by an aperture with a conspicuous raphe canal in the condyle as in *Cleyera*? *variabilis*. Hilum at the extremity of the condylar cavity. The maximum breadth of the condyle (1·14 mm.) is exaggerated by bursting along the raphe canal. Breadth of testa measured on the suture plane about 0·2 mm. near the hilum and on the outer side of the chalazal limb; 0·7 mm. on the outer side of the micropylar limb. Structure of testa in section somewhat obscure owing to decay, but apparently formed of small rectangular cells about 0·018 mm. in diameter. External surface of testa ornamented with coarse rounded tubercles of irregular outline many at least 0·1 mm. in diameter. (The whole surface much obscured by decay and too brittle for satisfactory cleaning.) Locule lining transversely striate, cell-structure obscure. Maximum diameter of seed, 3·75 mm.; diameter at right angles to it, 3 mm.

REMARKS. The seed is distinguished from other fossil species by the combined characters of large size and oblique orientation.

Family THYMELIACEAE

Genus *DAPHNE* Linnaeus

? *Daphne* sp.

(Pl. 34, figs. 125, 126)

DESCRIPTION. *Seed:* Pointed obovoid with a slight tumescence over the chalaza at the broad end which is pierced at the centre by a small aperture. Micropylar end pointed (slightly imperfect). Surface of integument (tegmen) black and shining formed of flat or scarcely inflated equiaxial cells each with a large pit at its centre which occupies at least half the diameter of the cell. Diameter of cells about 0·014 mm. The cells show some longitudinal alignment especially near the hilar end. The tegmen is about 0·08 mm. thick where it could be measured, columnar in section with curved columns. Length of seed, 2·25 mm.; breadth, 1·2 mm. About the same size as the species from Hengistbury but narrower and more attenuated to the base. The specimen is imperfect, the seed having cracked obliquely so that part of the testa is missing on one side.

Genus ?

(Pl. 34, figs. 127–129)

Two other fragments, probably Thymeliaceae, belong to another genus or other genera. One (Pl. 34, figs. 127, 128) shows a deep invagination over the chalaza. Where seen in section the wall is 0·1 mm. thick formed of straight columnar cells. Cells in surface view have median pits and although the surface is much decayed equiaxial cells can be distinguished about 0·05 mm. in diameter. Maximum breadth of seed preserved (near the chalazal end), 2 mm. A second fragment (Pl. 34, fig. 129) appears to belong to the family but is too poor for description. It lacks the marked invagination of the specimen in figs. 127, 128.

Family LYTHRACEAE

Genus ***DECODON*** J. F. Gmel.

Decodon gibbosus (E. M. Reid)

(Pl. 34, figs. 130–133)

1920. *Diclidocarya gibbosa* E. M. Reid, p. 82, pl. 4, figs. 23, 25.
1929. *Decodon gibbosus* (E. M. Reid) E. M. Reid, p. 37, pl. 589, figs. 8, 9.

DESCRIPTION. *Seed:* Bisymmetric, inverted pyramidal, sub-triangular in side view, narrowly triangular as seen from the ventral side, the breadth in the dorsiventral plane of symmetry being greater than that at right angles to it. Angles and edges of pyramid rounded. Top of seed broad, sloping to the back, base somewhat roundly truncate, dorsal side with rounded longitudinal angle. Ventral side with flat or slightly concave triangular germination valve which may end in a sharp mucro below. Dehiscence begins at the pointed end and continues up the sides of the valve which, however, remains attached to the endocarp at the broad upper end. Surface of valve with several longitudinal lines of square cells or pits about 0·025–0·03 mm. in diameter. Six lines of these cells were visible in one specimen but this surface may be partially or wholly obscured by a thin epidermis showing longitudinal striations and fine equiaxial cells about 0·012 mm. in diameter. The cells tend to diverge from the basal hilar-micropylar area. Thickness of testa on dorsal side of spongy equiaxial cells also about 0·012 mm. in diameter. Dimensions of seeds as follows: 1) Length, 1·1 mm.; maximum breadth of ventral face, 0·7 mm. Breadth of valve at upper end, 0·45 mm.; dorsiventral maximum breadth near apex, 0·825 mm. 2) Length, 0·95 mm.; maximum breadth of ventral face, 0·825 mm.; and of valve, 0·45 mm. Length of valve about 0·6 mm.; dorsiventral maximum breadth, 1 mm. 3) Length, 1·05 mm.; maximum breadth of ventral face, 0·7 mm.; and of valve, 0·5 mm; dorsiventral maximum breadth, 0·8 mm.

Remarks. Three seeds which appear indistinguishable from *D. gibbosus* (E. M. Reid), a species originally described from the Mio-Pliocene of Pont-de-Gail under the generic name *Diclidocarya* (1920: 82, pl. 4, figs. 23, 25. See also E. M. Reid, 1929: 37, pl. 589, figs. 8, 9). Later P. A. Nikitin referred *Diclidocarya globosa* to the living genus *Decodon* (1929: 33–36, pl. 589) to which also *Diclidocarya gibbosa* belongs. The Pont-de-Gail seeds are slightly larger than the Barton (length, 1·2–1·4 mm.; breadth, 1·2–1·4 mm.) but in many-seeded fruits such as *Decodon* slight differences of size may be of relatively little significance. This is the first fossil occurrence of the living genus so far recorded in English strata.

Genus ***DICLIDOCARYA*** E. M. Reid, 1920: 82

Diclidocarya minor n. sp.

(Pl. 34, figs. 134–137)

Diagnosis. Seed broadly-ovate in outline, 0·75–0·85 mm. long, 0·8–0·95 mm. broad, much compressed. Germination valve elliptical. Seed-body, distinct on the ventral surface, flanked by a spongy thickening on each side from which it is separated by a groove.

Holotype. Brit. Mus. (N.H.), No. V.36459.

Description. *Seed:* Bisymmetric, broadly oval (or roundly triangular) in outline, somewhat compressed in the direction of the plane of symmetry. Seed-body median, longitudinal, more or less fusiform, flanked on each side by a spongy thickening of the testa formed of equiaxial cells, 0·016 mm. in diameter. Operculum or germination valve as in *D. menzelii*, ellipsoid covering the lower half of the seed-body on the dorsal side. On germination the valve becomes completely detached (unlike *Decodon*) and in both specimens it had already fallen. Ventral surface with a marked broad subfusiform median ridge associated with the seed-body. Maximum breadth of ridge, 0·15–0·2 mm. Ridge separated from the lateral thickenings by a longitudinal groove on each side. Longitudinal striae on the median line of the seed-body may indicate the position of the raphe. Surface much abraded but in the holotype fine fibre-like cells are seen surrounding the plug aperture and swirling over the surface as in many Lythraceae. Length of seed, 0·75–0·85 mm.; breadth, 0·8–0·95 mm. Length of plug, 0·4–0·6 mm.; breadth, 0·2–0·3 mm.

Remarks. Two seeds, much sand-pitted with operculum fallen. Their position in the genus *Diclidocarya* is clearly indicated by the form of the seed with body flanked by spongy testa thickenings and ellipsoid operculum falling completely free.

They are markedly smaller than *D. menzelii* (with seeds 1·3–2·5 mm. long; 1·3–2·4 mm. broad), also the seed-body is more clearly distinguished from the lateral thickenings than in that species.

Genus ***PALAEOLYTHRUM*** nov.

DIAGNOSIS. Seed subcircular, obovoid or obovate with or without marginal rim, wings or other conspicuous features of the testa, with median ventral raphe and subapical chalaza. Inner integument with a rough coat of transversely elongate and aligned cells overlain by longitudinal fibres.

TYPE SPECIES. *Palaeolythrum bournense* n. sp.

Palaeolythrum bournense n. sp.

(Pl. 34, figs. 138, 139)

DIAGNOSIS. Seeds subcircular to obovate, bifacial with one slightly convex surface, the other flat or slightly concave, both surfaces having curved longitudinal ribs except on the broad rim which surrounds an obovate apiculate body. Anatropous with median ventral raphe and transversely striate tough inner integument. Seed-cavity shining, lined by equiaxial or oblong cells. Chalaza scar conspicuous, rimmed, on one surface at the broad extremity. Length of perfect seed, 2–2·25 mm.; breadth about 2 mm. Length of seed-body, 1·2–1·75 mm.; breadth, 0·9–1·3 mm.

HOLOTYPE. Brit. Mus. (N.H.), No. V.36487, from the Bournemouth Freshwater Beds at Branksome Dene, awaiting publication.

DESCRIPTION. *Seed:* Obovate (represented by seed-body), the testa having been largely or entirely removed by abrasion, bisymmetric, one broad surface being slightly concave, the other very slightly convex. Hilum at the narrow end (as demonstrated by Bournemouth material), chalaza indicated by a small deep rectangular depression on the concave surface at the opposite end of the seed to the hilum. The chalazal depression has a raised rim. One specimen (Pl. 34, fig. 138) shows longitudinally aligned slight rugosities, the remains of the outer integument, or testa, now abraded. This surface also shows longitudinal striations. From the other specimen the testa has been entirely worn away leaving only the remains of an inner coat of transversely aligned cells represented by their torn edges. They produce transverse striations except around the chalaza where they are concentric to this organ, crossing the margin of the seed-body at right angles and forming a slight rim around the sunk chalaza scar. Dimensions of seed-body: 1) Length, 1·75 mm.; breadth, 1 mm. 2) Length (less abraded specimen), 1·5 mm.; breadth, 1·15 mm.

REMARKS. These seed-bodies are identical with similarly abraded material from Sandbanks and Branksome Dene in the Bournemouth Freshwater Beds. The species also occurs in the Bournemouth Marine Beds. The relationship with Lythraceae is fully discussed by the writer in a forthcoming monograph where beautifully preserved material with testa intact is described. The mode of occurrence of these specimens which are abundant in fine silt together with Cyperaceae at Bournemouth suggests an aquatic or sub-aquatic habit which would be in keeping with the family Lythraceae.

Family Cornaceae

Section Mastixioideae

Genus ***EOMASTIXIA*** Chandler, 1926 : 37

Eomastixia rugosa (Zenker)

1833. *Baccites rugosus* Zenker, p. 12, pl. 1, figs. 9, 10.
1926. *Eomastixia bilocularis* Chandler, p. 37, pl. 6, fig. 6*a–e*.
1957. *Plexiplica rugosa* (Zenker) Kirchheimer, pp. 259–260, pl. 9, fig. 470 ; pl. 40, fig. 161*a–c*.

The species is redescribed and fully discussed in a forthcoming monograph of the Lower Bagshot flora where a complete list of synonyms is given. Dr. Kirchheimer has kindly examined some of the well-preserved endocarps from the Lower Headon of Hordle and is satisfied that they are identical with Zenker's species which he had described as *Plexiplica rugosa* (Zenker) before seeing the Hordle material.

Poorly preserved or rather perishable endocarps have been found from time to time in the Lower and Middle Bartonian. Typical examples are to be figured in the monograph referred to above. Two such were pyritized fruits collected by E. M. Reid and M. E. J. Chandler from the Middle Bartonian which showed the exocarp and superior perianth scar. The specimens were small and perhaps immature. Another specimen collected by W. Lennie Ames, also from the Middle Bartonian showed the endocarp with valves beginning to split both along their margins and along the median infolds. The subsequent decay of the carbonaceous endocarp revealed calcite locule-casts which reproduced the form of the two seeds.

A crushed three-loculed endocarp was found by E. St John Burton at Horizon A3, Lower Bartonian. It showed the three valves externally and, on being fractured, three locules were visible, all much compressed, one probably abortive. This specimen is referred to by Burton (1933 : 151) as an endocarp (allied to *Mastixia*).

All the specimens mentioned are now decayed. The genus is well known throughout the Hampshire and Dorset coast section from the Lower Bagshot to the Lower Headon of Hordle.

Family Epacridaceae

Genus ***EPACRIDICARPUM*** Chandler (see p. 214)

Epacridicarpum headonense n. sp.

(Pl. 34, figs. 146, 147)

1926. Ericaceae, Genus ? sp. 1, Chandler, p. 31, pl. 6, fig. 7*a*, *b*.

Diagnosis. Fruits suboblate-sphaeroidal loculicidal capsules with five one-seeded locules. Walls thick formed of parenchyma, axis fibrous. Length of fruit 0·55–1 mm. ; diameter, 0·1–0·15 mm.

HOLOTYPE. Brit. Mus. (N.H.), No. V.36485 from Highcliff Sands, Cliff End near Mudeford, Hampshire, awaiting publication.

DESCRIPTION. A slightly stipitate sub-turbinate or oblate-sphaeroidal syncarpous loculicidal capsule. Originally five-loculed now represented by two united loculicidal segments with remains of fibrous axis and one separate segment. The form, broadest near the apex and somewhat flattened on top, the rough irregularly pitted external surface (now much abraded), thick parenchymatous carpel walls, smooth shining locule lining with narrow elongate cells diverging from the subapical placenta at the top of the axis, unite these specimens with Epacridaceae. They agree with specimens from Cliff End near Mudeford and the Lower and Upper Headon Beds although the Barton specimens are small examples. No seeds seen. Length of longest fruit, 0·75 mm.; breadth across two united segments, 1·1 mm. Length of a smaller carpel, 0·55 mm.; breadth of a single segment, 0·5 mm.

? ***Epacridicarpum mudense*** Chandler

(Pl. 34, figs. 148–150)

See p. 214.

DESCRIPTION. *Fruit:* Loculicidal, approximately oblate-sphaeroidal but with greatest breadth below, syncarpous, five-carpelled, angled longitudinally over the locules, slightly concave over the septa. Locule lining smooth, cells diverging from subapical placentae on the inner angles: axis fibrous terminating at the apex in a broad flat-topped style. External surface very coarsely rugose also with deep pits. Length of fruit, 0·75 mm.; breadth (three carpels only), 1 mm. Length of a second fruit, 1 mm.; breadth (two carpels only), 1·4 mm. The fruits resemble those of *E. mudense* but are somewhat more markedly rugose in some instances.

Family SYMPLOCACEAE

Genus ***SYMPLOCOS*** Jacq.

Symplocos sp.

(Pl. 35, figs. 153, 154)

DESCRIPTION. A small inferior fruit with remains of persistent sepals and perianth disc. The sepals are so large that they suggest the fruit is immature. Fruit-body ovoid with unequally developed locules. Four gaping apertures at the apex indicate that these are four in number. Sepals appear to be bifid or lobed and probably arranged opposite to each locule but some are broken. Scar of attachment subbasal, slightly asymmetrically placed. From it a few furrows diverge up the sides of the fruit. Septa with a median plane of weakness along which there is a tendency to split. Where the planes intersect there is a central canal. Length of fruit including sepals, 3·25 mm.; breadth, 2·2 mm.

REMARKS. The inferior fruit with apical perianth disc and locules opening at the apex indicates *Symplocos*. The immature condition does not permit of closer determination.

Family ?

Genus ***RHAMNOSPERMUM*** Chandler (see p. 216)

Rhamnospermum bilobatum Chandler

(Pl. 35, figs. 155, 156)

See p. 216.

The characteristic bilobed "seeds" are fairly abundant in different stages of abrasion. Some, especially the more inflated specimens, show the outer coat. Others retain only the semi-translucent tegmen. Seeds very variable in size. Typical dimensions are shown by two figured specimens: 1) Length, 1·8 mm.; breadth, 2·5 mm. 2) Length, 3 mm.; breadth (lobes folded more or less upon themselves), 2·5 mm.

INCERTAE SEDIS

Carpolithus sp.

(Pl. 35, figs. 157–162)

DESCRIPTION. *Seed*: Ellipsoid, having a large gaping aperture at one end (chalaza? or embryotega aperture). At the opposite end are two small holes side by side whose purpose is not clear (Pl. 35, fig. 158 at *a*). Surface of small slightly convex equiaxial cells, 0·016 mm. in diameter. Sections of the wall show these cells to be the ends of oblique columns as in Thymeliaceae or Euphorbiaceae. Thickness of wall about 0·075 mm. The seeds show some tendency to be slightly lobed longitudinally. One seed shows three shallow furrows extending for about half to three-quarters of the length from the large aperture (cf. Pl. 35, fig. 159). Length of seeds about 2·25 mm.; breadth, 1·75 mm.; diameter of large aperture, 0·75 mm. Although the columnar coat recalls Thymeliaceae, the large aperture is unlike anything seen in this family.

Carpolithus sp.

(Pl. 35, fig. 163)

A subglobular body (seed?) ornamented with a sharp network of ridges between which are deep hollows. The ridges are irregularly serrated. The hollows are polygonal and more or less equiaxial in outline; typical hollows measure 0·1 and 0·17 mm. in diameter. A second broken specimen shows the inner surface which is light brown with irregular pock marks with no clear cell structure and somewhat spore-like in texture. Outer surface dark having a metallic appearance. No spore-like triradiate mark seen. Dr. J. W. Franks kindly examined it and states that it is not a spore. Dimensions: 1 × 0·9 mm.

Carpolithus sp.

(Pl. 35, fig. 164)

Seed transversely oval with broad surfaces and rounded margins. One surface markedly convex, the other with two unequal facets separated by an oblique angle as if caused by pressure of other seeds in a fruit. At the middle of one long margin is a round deep foramen (micropyle?), about 0·17 mm. in diameter. Surface smooth and somewhat shining, its cell structure obscure. The appearance suggests a thin epidermis covering a thick corky coat and perhaps only a narrow longitudinal seed-cavity. Length, 1 mm.; breadth, 1·5 mm.; thickness, 0·6 mm. The specimen has not been identified.

Carpolithus sp.

(Pl. 35, figs. 165–167)

A semi-globose organism, excavated deeply on the flat side, having a series of branching furrows diverging from a central point on the rounded side and extending to the margin of the hollowed face. The specimen was cracking concentrically and radially. Its subsequent disintegration showed numerous cavities radiating from the centre of the rounded surface. All were filled with matrix. Indications of these cavities can be seen on the lower margin of fig. 167. The nature of this body is obscure, possibly it was a compound fruit with associated bracts. Height, 6·5 mm. Diameter, 9·25 × 8·25 mm.

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PLATE 29

Araucarites sp. (? *Araucarites sternbergi* Goeppert)

Fig. 1. Twig. × 6·5. Marine clays between 22 and 40 ft. above basal pebble bed.

Fig. 2. Thick twig with broken and abraded leaf-tips. × 6·5. Marine clays 19 ft. above basal pebble bed.

Fig. 3. Detached leaf. × 14. Marine clays 40 ft. above basal pebble bed.

All Upper Hengistbury Beds, south-east face, Hengistbury Head.

All the above destroyed in attempts to prepare cuticle.

Pinus sp.

Fig. 4. Leaf fragment, lower surface showing three longitudinal ridges. × 20. (V.36361.)

Fig. 5. Same, upper surface. × 20.

Fig. 6. Leaf fragment, upper surface, with six lines of stomata, having a single ridge on lower surface. × 20. (Destroyed in an attempt to prepare cuticle.)

Fig. 7. Leaf fragment, upper surface, with seven rows of stomata. × 20. (V.36362.)

Fig. 8. Fragment, lower surface, with single asymmetrically-placed ridge. × 20. (V.36363.)

Fig. 9. Same, upper surface, showing six lines of stomata. × 20.

Fig. 10. Fragment, upper surface showing seven lines of stomata. × 20. (V.36364.)

Fig. 11. Same, lower surface. × 20.

Figs. 4, 5, 7–11. Marine clays 25 ft. above basal pebble bed. Fig. 6. Marine clays 15 ft. above basal pebble bed.

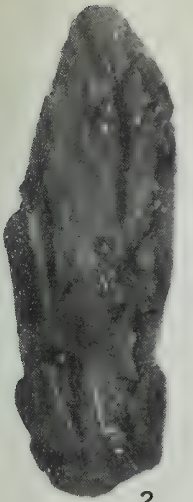
All Upper Hengistbury Beds, south-east face, Hengistbury Head.

Pinus dixoni (Bowerbank)

Fig. 12. Neotype. Cone, very slightly imperfect at base. × 1. (V.36352.)

Fig. 13. Same, opposite side. × 1.

Upper part of Lower Hengistbury Beds on shore at low-water mark. South-east face, Hengistbury Head.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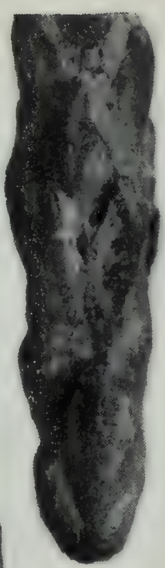
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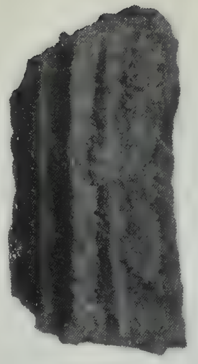
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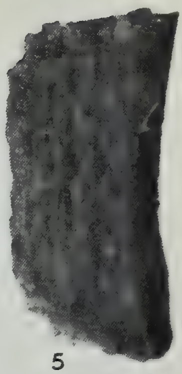
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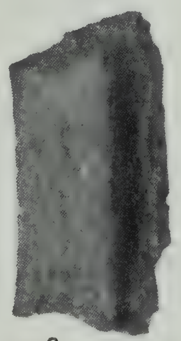
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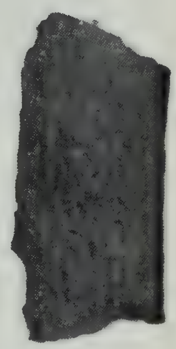
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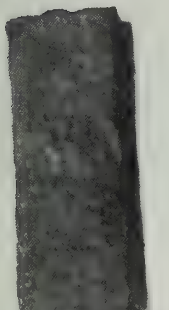
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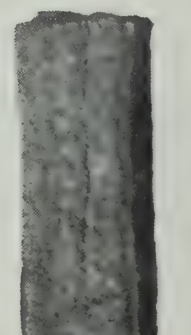
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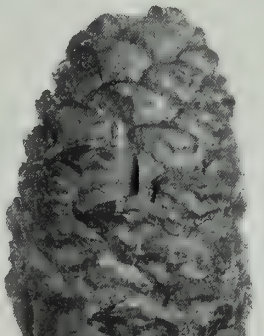
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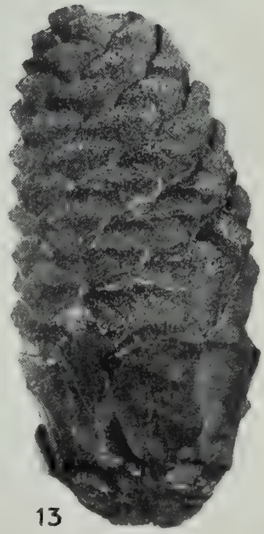
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PLATE 30

Pinus dixoni (Bowerbank)

FIG. 14. Lower part of cone in Pl. 29, fig. 12 showing character of the scale apophyses. × 2·7.

FIG. 15. Second more fragmentary cone. × 1. (V.36353.)

Both upper part of Lower Hengistbury Beds on shore at low-water mark. South-east face, Hengistbury Head.

Limnocarpus headonensis (Gardner)

FIG. 16. Ventrilateral aspect of a locule-cast. × 14. (Now decayed.)

FIG. 17. Same, lateral, condyle at (c). × 14.

Marine clays between 22 and 40 ft. above basal pebble bed, Upper Hengistbury Beds, south-east face, Hengistbury Head.

Stratiotes hantonensis n. sp.

Fig. 18. Valve of a seed showing external surface, sigmoidal form associated with a short raphe and small prominent collar (*c*) ; (*h*) hilum ; (*k*) keel. × 9·5. (V.36366.)

FIG. 19. Same, inner surface ; (*r*) short curved raphe ; (*h*) hilum ; (*m*) micropyle. × 9·5.

FIG. 20. Typical seed ; (*c*) collar with micropyle ; (*k*) keel. × 9·5. (V.36367.)

Both dark sands, cliff base, west end of Hengistbury Head.

FIG. 21. Relatively unworn seed. × 9·5. (V.36371.)

FIG. 22. Seed showing ridges and pits ; (*h*) hilum ; (*m*) micropyle. × 9·5. (V.36370.)

Both marine clays, 19 ft. above basal pebble bed.

FIG. 23. Small, somewhat abraded, compressed seed, ventrilateral view. × 9·5. (V.36369.)

FIG. 24. Same, dorsilateral view showing incipient separation of the two valves along the edge of the keel ; (*c*) collar. × 9·5.

Marine clays 40 ft. above basal pebble bed.

FIG. 25. An abraded seed showing collar smoothly rounded at (*c*) ; (*k*) keel. The margin is slightly broken above. × 9·5. (V.36372.) Marine clays 25 ft. above basal pebble bed.

All Upper Hengistbury Beds, south-east face, Hengistbury Head.

Scirpus lakensis n. sp.

FIG. 26. Abraded seed, inner coat only preserved. × 20. (V.36378.) Dark sands, cliff base, west end of Hengistbury Head.

Caricoidea obscura n. sp.

FIG. 27. Fruit, side. × 14. (V.36380.)

FIG. 28. Another (broken or bitten by animal at top right). × 14. (V.36384.)

FIG. 29. Endocarp released from a fruit. × 14. (V.36381.)

FIG. 30. Another endocarp partly surrounded by broken fruit. × 14. (V.36382.)

FIG. 31. Another fruit (excrescence (*e*) a patch of pyrites). × 14. (V.36383.)

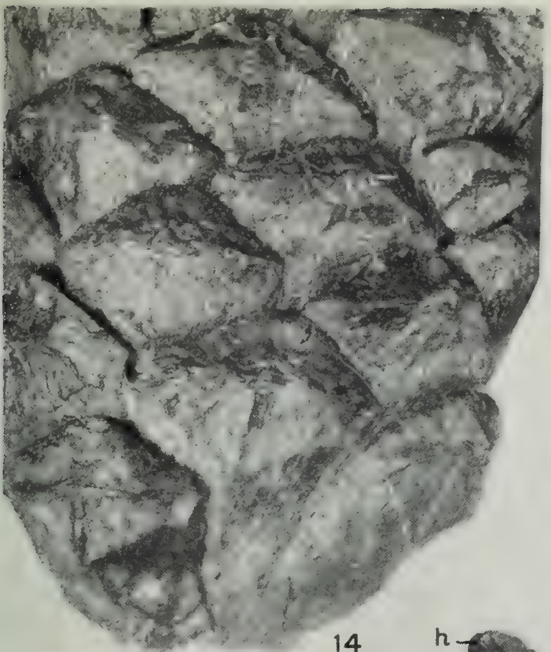
FIG. 32. Another fruit with adherent tissue (bract ?) on right below. The whole surface is encrusted with pyrites and cracked. × 14. (Now decayed.)

FIG. 33. Smaller crushed fruit (immature ?) with exocarp preserved. × 14. (V.36385.)

FIGS. 27, 29–31. Marine clays 19 ft. above basal pebble bed.
FIGS. 28, 32, 33. Marine clays 25 ft. above basal pebble bed.
Upper Hengistbury Beds, south-east face, Hengistbury Head.

FIG. 34. Endocarp with adherent remains of fruit at base giving the appearance of an expanded neck. May belong to this species. × 14. (V.36387.)

Dark sands, cliff base, west end of Hengistbury Head.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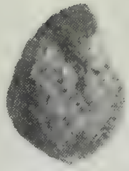
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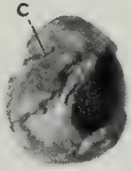

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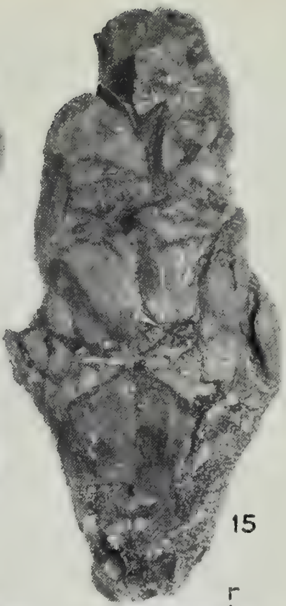
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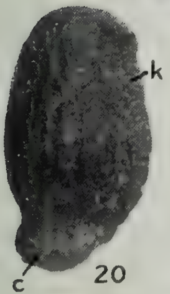

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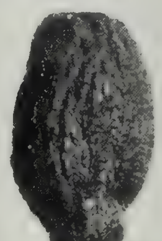
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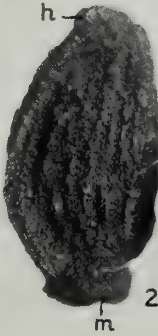

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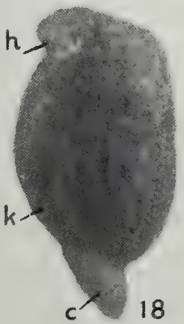

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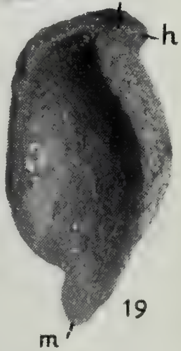

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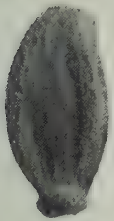
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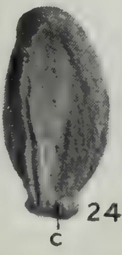

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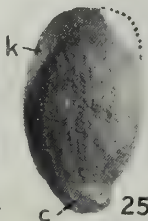

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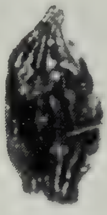
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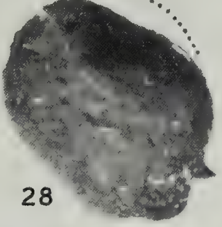
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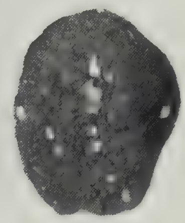
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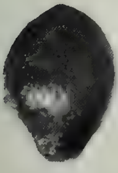
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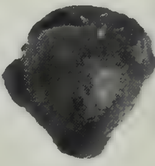
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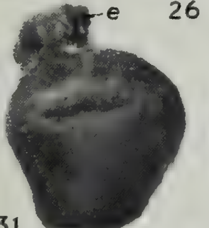

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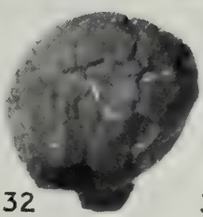
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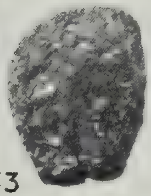
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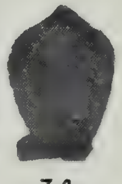
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Caricoidea maxima n. sp.

FIG. 35. Holotype, fruit, side. ×14. (V.36388.) Marine clays 40 ft. above basal pebble bed, Upper Hengistbury Beds, south-east face, Hengistbury Head.

Palmophyllum sp.

FIG. 36. Fragment of leaf with pinnae arising from axis. ×9·5. (V.36389.)

FIG. 37. Same, opposite side. ×9·5.

Marine clays 40 ft. above basal pebble bed, Upper Hengistbury Beds, south-east face, Hengistbury Head.

MORACEAE, Genus ?

FIG. 38. Fruit, broken transversely, (*st*) style; (*f*) funicle where it enters to placenta. × 20. (V.36390.) Marine clays 19 ft. above basal pebble bed, Upper Hengistbury Beds, south-east face, Hengistbury Head.

Hantsia pulchra (Chandler)

FIG. 39. Seed, broken and distorted. ×14. (V.36391.) Marine clays 25 ft. above basal pebble bed, Upper Hengistbury Beds, south-east face, Hengistbury Head.

Brasenia ovula (Brongniart)

FIG. 40. Pointed-oval seed with embryotega (*e*). ×14. (V.36392.) Dark sands, cliff base, west end of Hengistbury Head.

FIG. 41. Broader seed with aperture (*a*) (split) for lost embryotega. ×14. (V.36393.)

Marine clays between 22 and 40 ft. above basal pebble bed, Upper Hengistbury Beds, south-east face, Hengistbury Head.

Palaeobursera sp.

FIG. 42. Pyrene, dorsal. (*v*) Position at margin of lower end of germination valve (much obscured by adherent tissue). × 20. (V.36396.)

FIG. 43. Same, ventral showing short, upward curved aperture (*a*) for entry of funicle. ×20.

Marine clays 25 ft. above basal pebble bed, Upper Hengistbury Beds, south-east face, Hengistbury Head.

Vitis sp.

FIG. 44. Seed, ventral with short, sub-parallel infolds and stipitate base. ×6·5. (Now decayed.)

FIG. 45. Same, dorsal with small oval chalaza situated somewhat above the middle. ×6·5.

Dark sands, cliff base, west end of Hengistbury Head.

Daphne sp.

FIG. 46. Seed, side (broken at hilar end). ×15. (Now decayed.)

FIG. 47. Same, opposite side, tilted to show chalaza (small circular foramen). ×15. Marine clays 19 ft. above basal pebble bed, Upper Hengistbury Beds, south-east face, Hengistbury Head.

Cleyera ? *variabilis* (Chandler)

FIGS. 48, 49. Two seeds. ×14. (V.36397, V.36398.)

Dark sands, cliff base, west end of Hengistbury Head.

FIGS. 50–53. Four seeds. ×14. (V.36400–V.36403.)

FIG. 54. Seed showing curved limbs clearly emphasized by distortion. ×14. (V.36404.)
All marine clays 19 ft. above basal pebble bed.

FIG. 55. Small distorted seed. ×14. (V.36406.)

FIG. 56. Another small seed. ×14. (V.36407.)
Both marine clays between 22 and 40 ft. above basal pebble bed.
All Upper Hengistbury Beds, south-east face, Hengistbury Head.

Epacridicarpum mudense n. sp.

FIG. 57. Two united carpels showing two locules (*l*, *l*). (Left hand locule almost hidden behind septum.) ×14. (V.36409.)

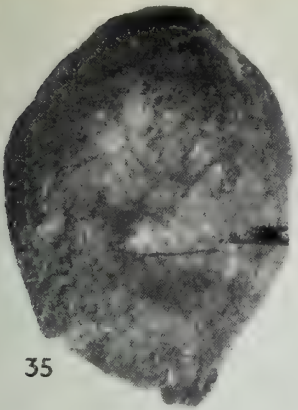
Marine clays between 22 and 40 ft. above basal pebble bed, Upper Hengistbury Beds, south-east face, Hengistbury Head.

Symplocos sp. (? *Symplocos headonensis* Chandler)

FIG. 58. Endocarp, side, slightly distorted so that part of the apical depression is shown with apertures leading into locules. ×6. (V.36410.)

FIG. 59. Same, apex, showing obscurely the apical depression (flattened) with three of the four locules (*l*, *l*) and central canal (*c*). ×6.

Marine clays 19 ft. above basal pebble bed, Upper Hengistbury Beds, south-east face, Hengistbury Head.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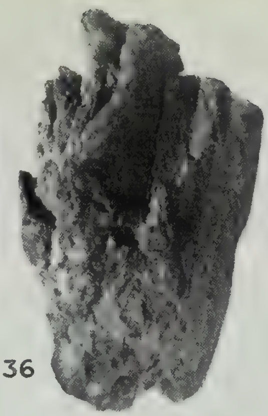
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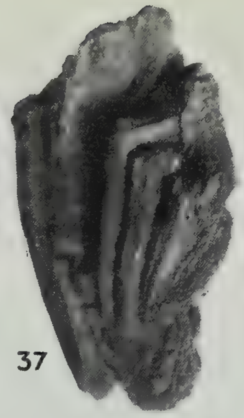
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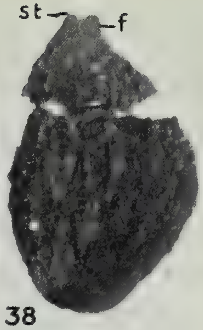

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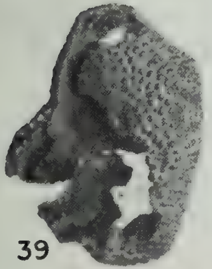
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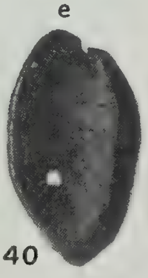

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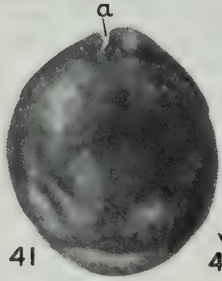

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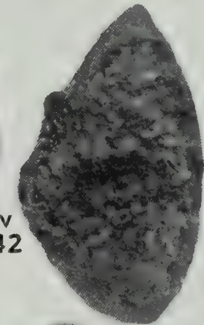

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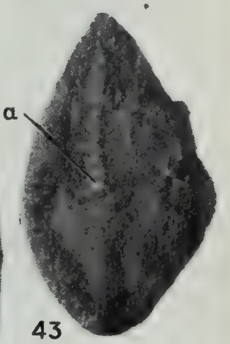

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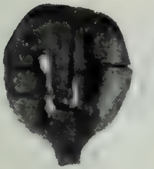
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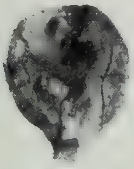
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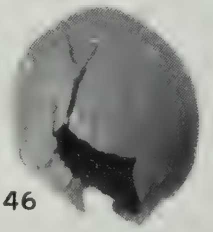
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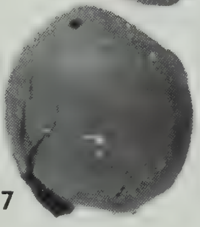
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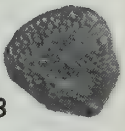
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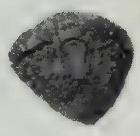
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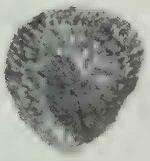
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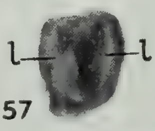

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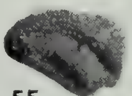
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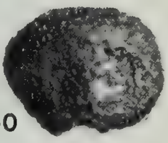
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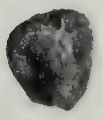
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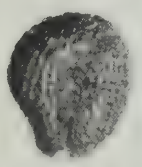
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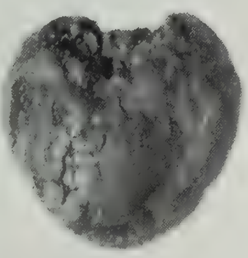
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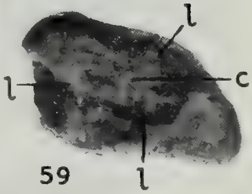

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PLATE 32

Rhamnospermum bilobatum Chandler

FIG. 60. Laterally flattened seed. The dorsal lobes lie one upon the other (left). × 14. (V.36411.)

Marine clays 25 ft. above basal pebble bed, Upper Hengistbury Beds, south-east face, Hengistbury Head.

FIG. 61. Much abraded seed with only inner integument preserved. One dorsal lobe is seen towards base of figure overlain at (*o*) by the other lobe. Dorsal side to right. × 14. (V.36415.)

Dark sands, cliff base, west end of Hengistbury Head.

Carpolithus cornutus n. sp.

FIG. 62. Spiney fruit. (*a*) Attachment; (*ap*) apex. × 9·5. (V.36418.)

FIG. 63. Same, opposite side showing incipient splitting into two valves. (*a*) Attachment; (*ap*) apex. × 9·5.

FIG. 64. Holotype. × 9·5. (V.36417.)

FIG. 65. Immature specimen with bracts or perianth lobes forming spines incompletely fused. × 9·5. (Now decayed.)

All marine clays between 22 and 40 ft. above basal pebble bed.

FIG. 66. Immature specimen. This species? × 9·5. (V.36419.) Marine clays 40 ft. above basal pebble bed.

All Upper Hengistbury Beds, south-east face, Hengistbury Head.

Carpolithus spp.

FIG. 67. Fruit distorted to show bracteoles at apex. × 14. (V.36420.)

FIG. 68. Same, opposite side showing longitudinal ribs. × 14.

Marine clays 19 ft. above basal pebble bed.

FIG. 69. Tip of a large endocarp with smooth rim and coarse rugosities on the surface. × 14. (V.36421.)

Marine clays 25 ft. above basal pebble bed.

FIG. 70. Two-loculed endocarp, exterior (broken below). Two small depressions (*a*, *a*) are apertures leading into the locules. × 14. (V.36422.)

FIG. 71. Another fragment. × 14. (V.36423.)

Both marine clays between 22 and 40 ft. above basal pebble bed.

All Upper Hengistbury Beds, south-east face, Hengistbury Head.

FIG. 72. Fruit with three styles (inner layers only preserved). × 14. (V.36425.)

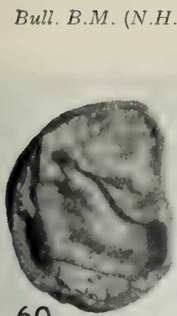
Dark sands, cliff base, west end of Hengistbury Head.

Pinus sp. (? *Pinus bowerbanki* (Carruthers))

FIG. 73. Crushed cone (slightly imperfect). × 1·1. (Now decayed.)

FIG. 74. Same, opposite side. × 1·1.

Middle Bartonian, Horizon C, Barton cliffs.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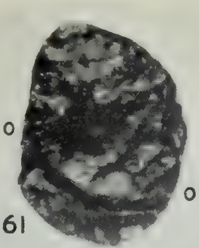

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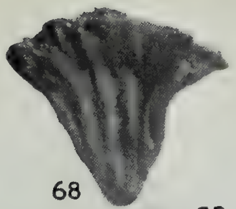
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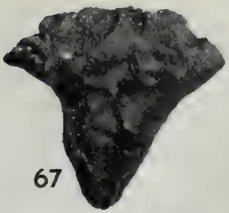
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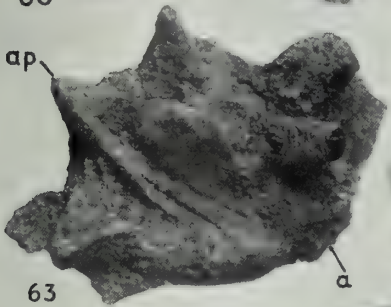

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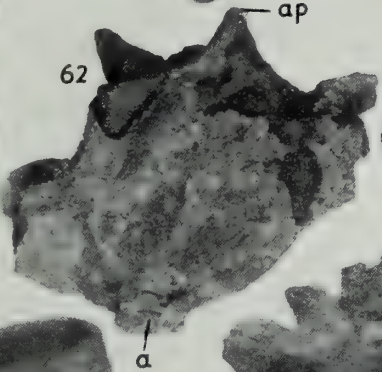

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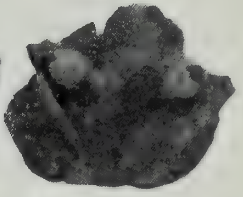
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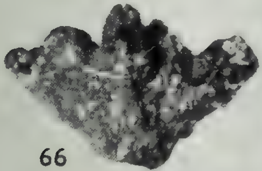
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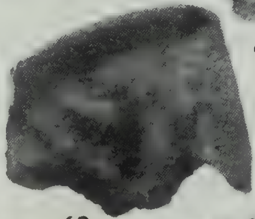
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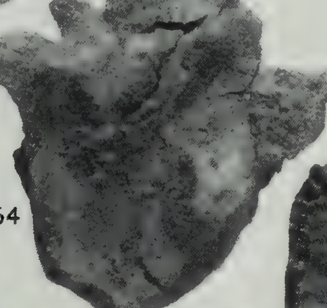
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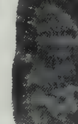
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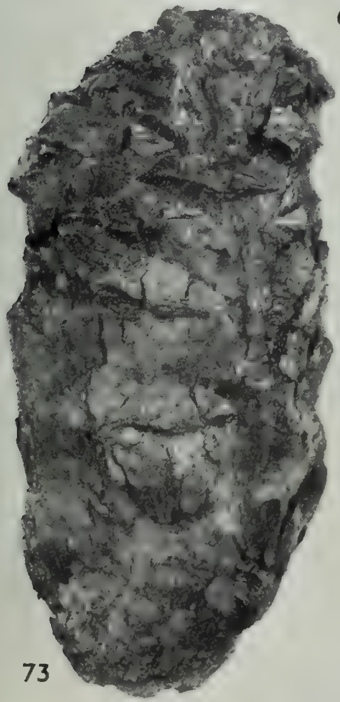
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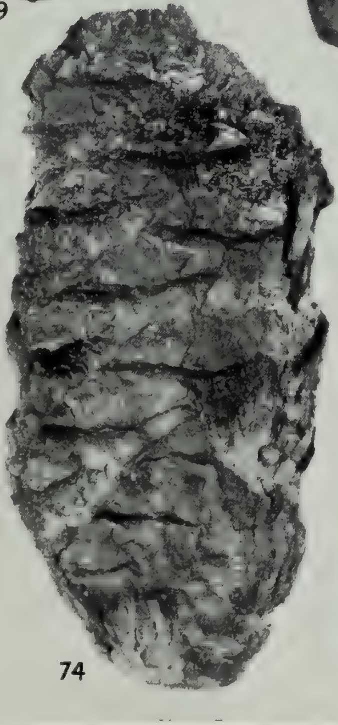
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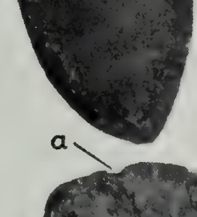
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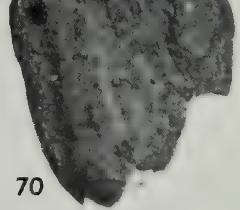

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PLATE 33

Pinus sp. (? *Pinus dixoni* (Bowerbank))

Figs. 75–79. Detached scales of a cone (now decayed). Figs. 75 and 76, opposite surfaces of one scale, fig. 75 being the lower surface. Figs. 77–79, the lower surfaces of three other scales. ×2.

Middle Bartonian, Horizon D, Barton cliffs.

Sequoia couttsiae Heer

Fig. 80. Fragment of twig. ×14. (Now decayed.)

Lower Bartonian, Horizon A, Highcliff.

Fig. 81. Another (destroyed in attempt to prepare cuticle). ×6·5.

Upper Bartonian, Horizon L, west of Beckton Bunny, Barton cliffs.

Coniferae, Genus ?

Figs. 82, 83. Two minute twig fragments. ×14. (Now decayed).

Lower Bartonian, Horizon A3, Highcliff.

Limnocarpus headonensis (Gardner)

Fig. 84. Locule-cast, side. Aperture for keel (missing) on right; (*c*) condyle. ×15. (V.36427.)

Fig. 85. Same, ventral. (*c, c*) Casts of condyle; (*a*) attachment. ×15.

Fig. 86. Another cast with cast of keel on right; (*c*) condyle. ×15. (V.36428.)

Both Upper Bartonian, Horizon K (Long Mead End Bed),Taddiford, Hordle Cliff.

Stratiotes hantonensis Chandler

Fig. 87. Valve of seed, external surface (broken at apex). ×6·5. (V.36429.)

Fig. 88. Another, internal surface. ×6·5. (V.36430.)

Both Lower Bartonian, Horizon A2, Highcliff.

Fig. 89. Valve of seed, exterior showing hooked form; (*c*) collar; (*k*) keel. ×8·5. (V.36431.)

Fig. 90. Same, interior, with long raphe near margin of keel (*k*); (*ch*) chalaza; (*h*) hilum; (*c*) collar. ×8·5.

Fig. 91. Micropylar end of a broken seed; (*c*) collar. ×8·5. (V.36432.)

Fig. 92. Valve (incomplete at apex), external surface; (*c*) collar. ×8·5. (V.36433.)

Fig. 93. Same, inner surface. ×8·5.

Fig. 94. Valve, exterior, showing sigmoidal form. ×8·5. (V.36434.)

Fig. 95. Same, inner surface showing short transverse raphe near apex of keel and subapical hilum (*h*); (*m*) micropyle. ×8·5.

All Lower Bartonian, Horizon A3, Highcliff.

Stratiotes headonensis Chandler

Fig. 96. Broken valve of seed, exterior, micropylar end missing. Shows ridged surface and broad flat keel. ×6·5. (V.36437.)

Fig. 97. Same, inner surface, broad keel on right bearing long marginal raphe. ×6·5.

Upper Bartonian, Horizon L, between "Black Bands", west of Beckton Bunny, Barton cliff.

Caricoidea obscura Chandler

Fig. 98. Fruit, side. ×14. (V.36438.)

Fig. 99. Another. ×14. (V.36439.)

Fig. 100. Mucronate endocarp protruding from remains of fruit (*f*) only preserved near base. ×14. (V.36440.)

Fig. 101. Similar but smaller specimen. ×14. (Now decayed.)

FIGS. 102–104. Endocarps, released from fruits. × 14. (V.36441–V.36443.)

FIG. 105. Endocarp with adherent fragments of fruit. × 14. (V.36444.)

All Lower Bartonian, Horizon A3, Highcliff.

Brasenia ovula (Brongniart)

FIG. 106. Small seed with gaping aperture (*a*) formerly closed by an embryotega. × 15. (V.36446.)

Upper Bartonian, Horizon K, east of Beckton Bunny, Hordle Cliff.

FIG. 107. Large seed (*a*) as in fig. 106. × 15. (V.36448.)

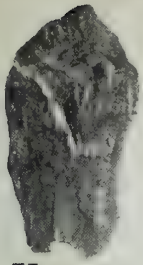
Upper Bartonian, Horizon L, between "Black Bands", west of Beckton Bunny, Barton cliff.

CAPPARIDACEAE or THEACEAE ? Genus ?

FIG. 108. Imperfect seed, exterior, showing unequal limbs, deep emargination between them, and foveolate surface. × 20. (V.36450.)

FIG. 109. Same, opposite side looking into curved seed-cavity. × 20.

Lower Bartonian, Horizon A3, Highcliff.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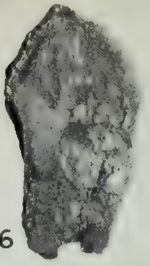
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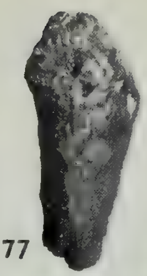
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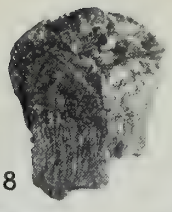
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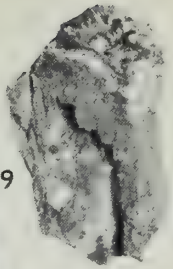
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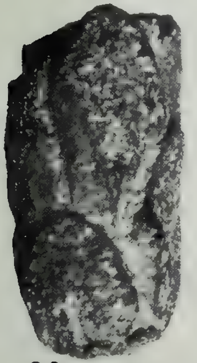
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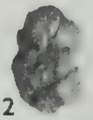
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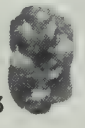
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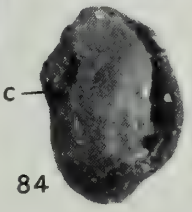

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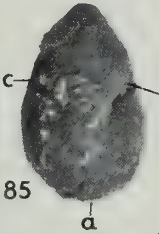

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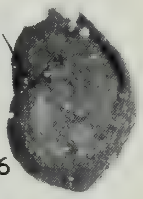
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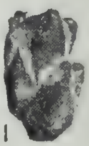
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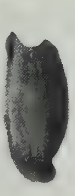
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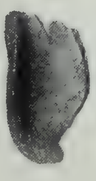
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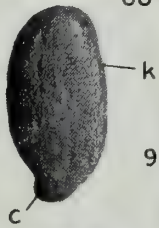

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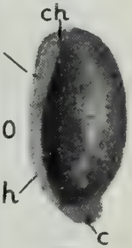

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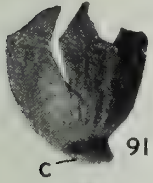

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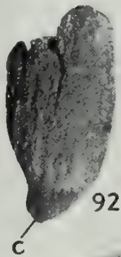

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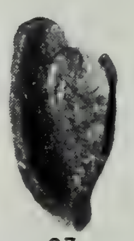
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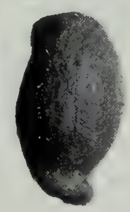
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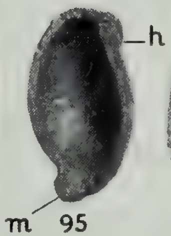

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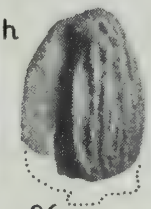
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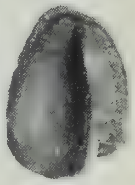
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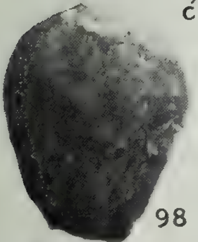
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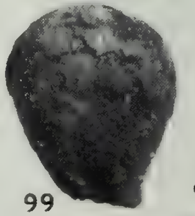
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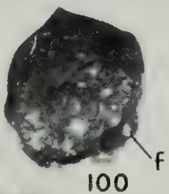

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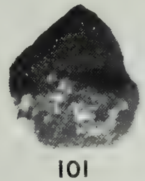
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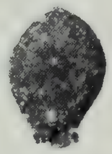
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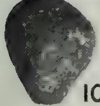
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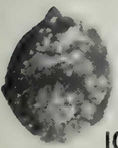
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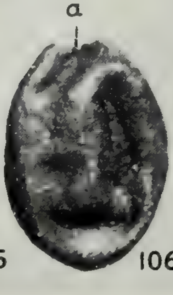

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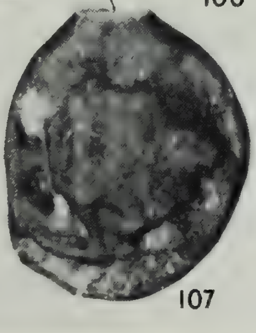

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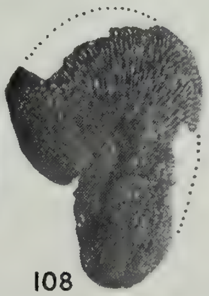
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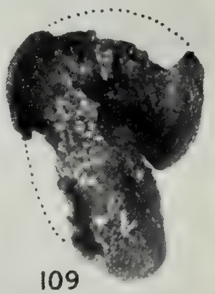
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Anonaspermum sp.

FIG. 110. Seed, exterior with cracked testa part of which has come away below on the left exposing ruminate albumen at (*a*). × 2·8. (Now decayed.)

FIG. 111. Same, opposite side. The specimen had split longitudinally through the albumen parallel with plane of symmetry, hence albumen is seen from the inside. × 2·8.

FIG. 112. Part of the other half of the split albumen, outer surface showing ruminations. × 2·8.

FIG. 113. Same, inner surface. × 2·8.

Bartonian of Barton cliff or Highcliff (precise horizon not known).

Rutaspermum sp.

FIG. 114. Seed, side ; (*v*) ventral margin. × 6·5. (V. 36451.)

FIG. 115. Same, looking onto ventral margin with large but narrow triangular hilar scar in the upper two-thirds. × 6·5.

Lower Bartonian, Horizon A2, Highcliff.

Rutaspermum sp.

FIG. 116. Seed, side ; (*v*) ventral edge ; (*ch*) probable position of chalaza. × 2·8. (Now decayed.)

FIG. 117. Same, ventral margin, with broad hilar scar. × 2·8.

Bartonian of Barton cliff (horizon not known).

Icacinicarya pygmaea n. sp.

FIG. 118. Endocarp, apex. Funicle ridge median in upper half of figure, flanked at apex (centre of figure) by two canals of which the apertures can be distinguished. × 14.

FIG. 119. Holotype. Another, side. Funicle on right. × 14.

FIG. 120. Another as in fig. 118. × 14.

FIG. 121. Another, side. Funicle on left. × 14.

All Lower Bartonian, Horizon A3, Highcliff. All now decayed.

Icacinicarya bartonensis n. sp.

FIG. 122. Holotype. Endocarp, apex. Funicle above, apertures of canals which flank it seen as two white spots. × 14. (V.36452.)

Upper Bartonian, Horizon K (Long Mead End Bed), Taddiford, Hordle Cliff.

ICACINACEAE, Genus ? (? *Natsiatum eocenicum* Chandler)

FIG. 123. Fragment of large endocarp with network of external ridges, part of rimmed margin on right. × 8·5. (V.36454.)

Lower Bartonian, Horizon A3, Highcliff.

Stizocarya sp.

FIG. 124. Endocarp, side, showing small circular scars due to hair-bases. × 6·5. (Now decayed.)

Middle Bartonian, Barton cliff (horizon not known).

? *Daphne* sp.

FIG. 125. Seed broken obliquely so that apex and base are separated. External surface. Small aperture (white) at apex = chalaza. × 14. (V.36455.)

FIG. 126. Same, reverse of imperfect seed showing cavity. (*ch*) Slight tumescence marking chalaza ; (*m*) micropyle. × 14.

Lower Bartonian, Horizon A3. Highcliff.

THYMELIACEAE, Genus ?

FIG. 127. Fragment of seed with deep invagination over chalaza. ×14. (Now decayed.)
FIG. 128. Same, reversed showing interior and wall in section. ×14.
FIG. 129. Chalazal end of a seed. Interior of fragment of testa. ×14. (Now decayed.)
Both Lower Bartonian, Horizon A3, Highcliff.

Decodon gibbosus (E. M. Reid)

FIG. 130. Side view of seed, germination valve beginning to gape on left. ×14. (V.36456.)
FIG. 131. Same, opposite side. ×14.
FIG. 132. Another seed, valve on right. ×14. (V.36457.)
FIG. 133. Another, ventrilateral, valve to left. ×14. (V.36458.)
All Lower Bartonian, Horizon A3, Highcliff.

Diclidocarya minor n. sp.

FIG. 134. Holotype. Seed, dorsal, operculum (in lower half) missing. ×20. (V.36459.)
FIG. 135. Same, ventral, showing median longitudinal ridge of raphe. ×20.
FIG. 136. Another seed, dorsal. Operculum missing. Testa broken above showing seed-cavity in crack. ×20. (V.36460.)
FIG. 137. Same, ventral, showing raphe. ×20.
Both Lower Bartonian, Horizon A3, Highcliff.

Palaeolythrum bournense n. sp.

FIG. 138. Seed abraded, remains of testa represented by obscure longitudinal ridges. ×20. (V.36461.)
FIG. 139. Another, opposite surface showing sub-terminal chalazal scar (*ch*). ×20. (V.36462.)
Both Lower Bartonian, Horizon A3, Highcliff.

Hordwellia crassisperma (Chandler)

FIG. 140. Typical seed. ×20. (V.36463.)
FIG. 141. Seed, distorted so that hilum faces camera. ×20. (V.36464.)
FIGS. 142, 143. Two larger seeds. ×20. (V.36465.) (That in fig. 143 now decayed.)
FIG. 144. Another. ×20. (V.36466.)
All Lower Bartonian, Horizon A3, Highcliff.

Cleyera ? *variabilis* (Chandler)

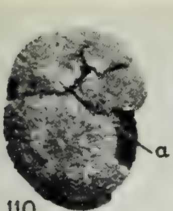
FIG. 145. Seed; (*h*) hilum. ×20. (V.36468.)
Lower Bartonian, Horizon A3, Highcliff.

Epacridicarpum headonense n. sp.

FIG. 146. Exterior of imperfect fruit, side. ×14. (V.36470.)
FIG. 147. Another valve of the same fruit, inner side showing septum between two locules (one in shadow). ×14.
Lower Bartonian, Horizon A3, Highcliff.

? *Epacridicarpum mudense* Chandler

FIG. 148. Exterior of incomplete fruit, side. Ridges overlie locules. ×14. (V.36471.)
FIG. 149. Exterior of another, side, splitting loculicidally. ×14. (V.36472.)
FIG. 150. Interior of part of a fruit showing two locules. ×14. (V.36473.)
All Lower Bartonian, Horizon A3, Highcliff.



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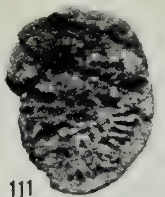
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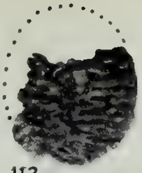
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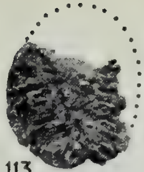
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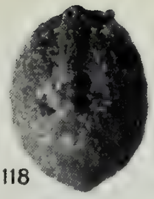
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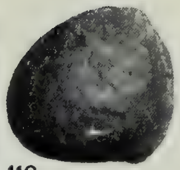
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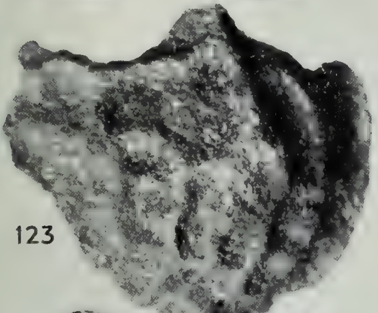
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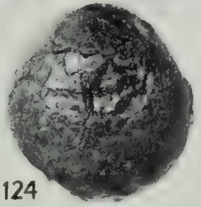
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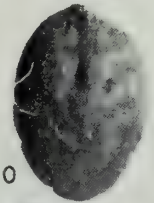
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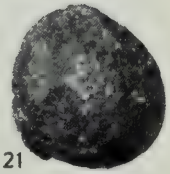
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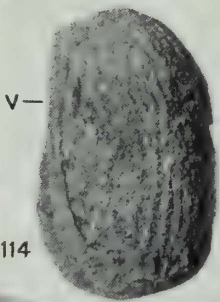

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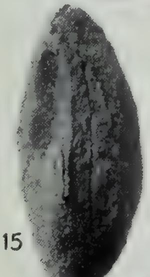
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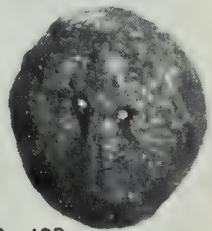
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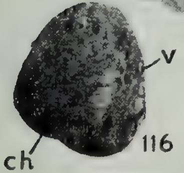

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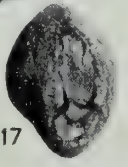
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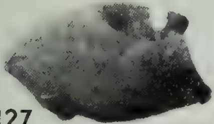
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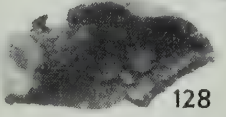
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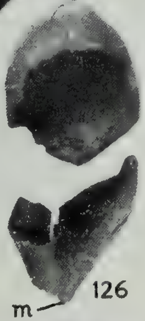

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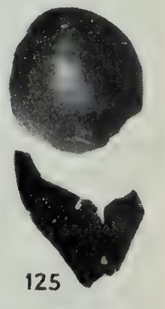
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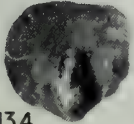
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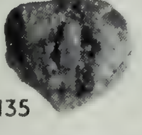
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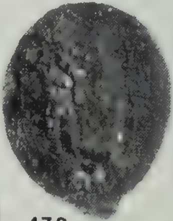
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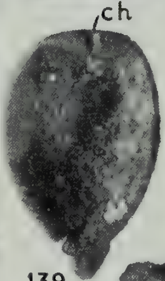

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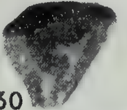
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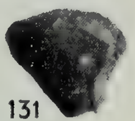
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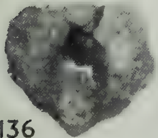
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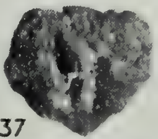
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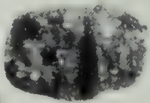
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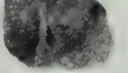
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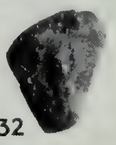
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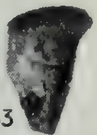
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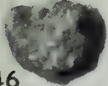
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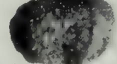
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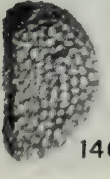
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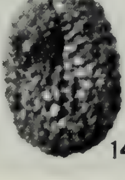
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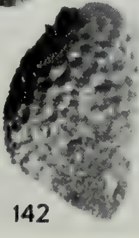
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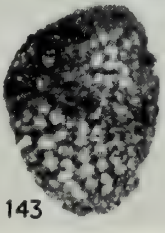
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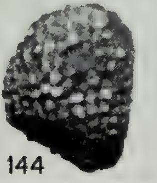
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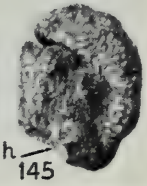

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PLATE 35

Cleyera ? bartonensis n. sp.

FIG. 151. Holotype. Valve of seed, external surface. × 6·5. (V.36469.)
FIG. 152. Same, inner surface showing obliquely oriented curved seed-cavity. × 15.
Lower Bartonian, Horizon A3, Highcliff.

Symplocos sp.

FIGS. 153, 154. Opposite sides of a young fruit with calyx still persisting. × 8·5. (V.36474.)
Lower Bartonian, Horizon A3, Highcliff.

Rhamnospermum bilobatum Chandler

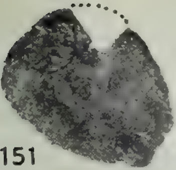
FIG. 155. Dorsilateral view of large crushed seed showing two lobes and pitted surface. × 15. (V.36475.)

Upper Bartonian, Horizon L, in sand between " Black Bands ", west of Beckton Bunny, Barton cliff.

FIG. 156. Dorsal view of small uncrushed seed. × 14. (V.36477.)
Lower Bartonian, Horizon A3, Highcliff.

Carpolithus spp.

FIG. 157. Seed tilted to show large terminal aperture. × 14.
FIG. 158. Another, opposite end to large aperture, showing two small foramina (*a*, *a*). × 14.
FIG. 159. Side of the same seed. × 14.
FIG. 160. Another seed, broken longitudinally, looking into cavity. × 14.
FIG. 161. Side of seed in fig. 157. × 14.
FIG. 162. Interior of another seed fragment showing columnar wall in section. White patches are sand grains. × 14.
All Lower Bartonian, Horizon A3, Highcliff. All now decayed.
FIG. 163. Small rounded seed with reticulate ornamentation. × 14. (V.36479.)
FIG. 164. Seed. (*f*) Foramen (micropyle ?). × 15. (V.36480.)
Both Lower Bartonian, Horizon A3, Highcliff.
FIG. 165. Side view of fruiting head (?) showing divergent furrows. × 7. (Now decayed.)
FIG. 166. Same, base. × 7.
FIG. 167. Same, apex showing hints of mud-filled cavities in rim near base of figure and the tendency to split along furrows parallel with a large central hollow. × 7.
Green glauconitic clay, Middle Bartonian, Barton cliff.



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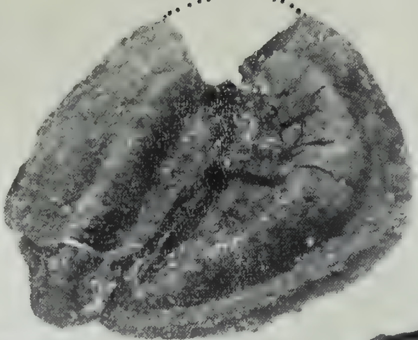

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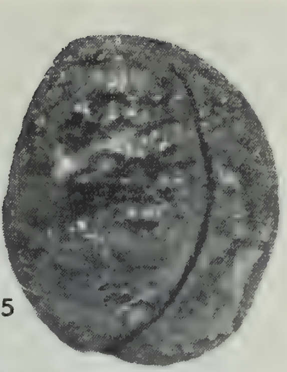

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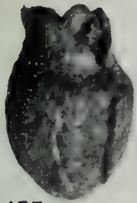

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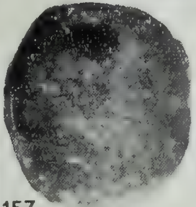

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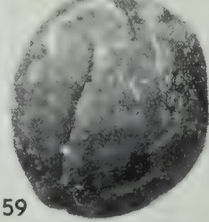

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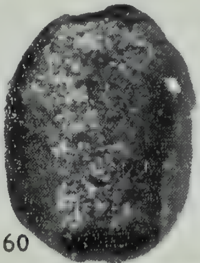

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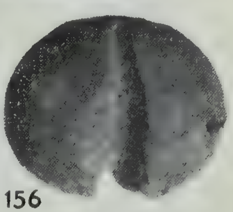

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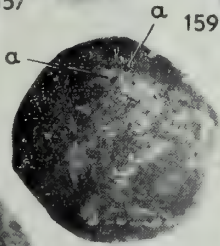

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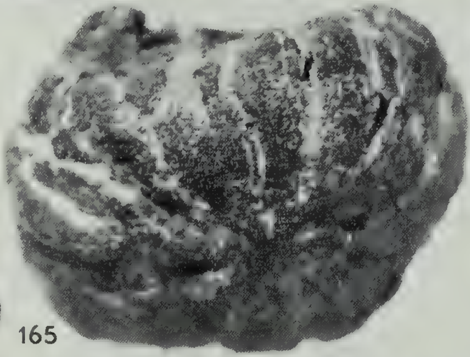

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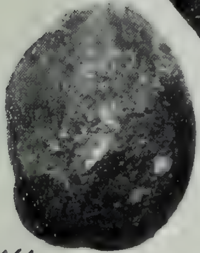

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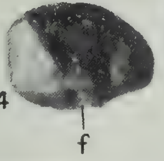

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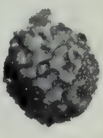

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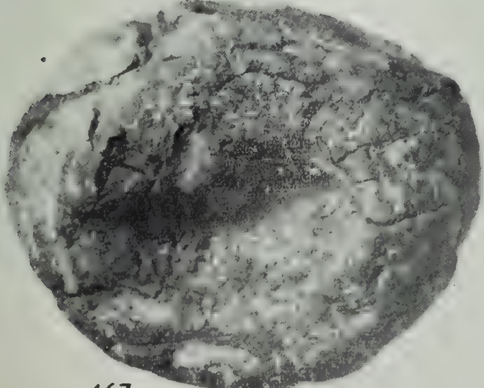

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A REVISION OF CERTAIN ACTINOPTERYGIAN AND COELACANTH FISHES, CHIEFLY FROM THE LOWER LIAS

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B. G. GARDINER

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A REVISION OF CERTAIN ACTINOPTERYGIAN AND COELACANTH FISHES, CHIEFLY FROM THE LOWER LIAS

BY

BRIAN GEORGE GARDINER

(Queen Elizabeth College, London

Pp. 239–384 ; *Plates* 36–43 ; 81 *Text-figures*

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A REVISION OF CERTAIN ACTINOPTERYGIAN AND COELACANTH FISHES, CHIEFLY FROM THE LOWER LIAS

By B. G. GARDINER

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SYNOPSIS

A redescription of part of the fish fauna of the Lower Lias is given, supplemented by an account of relevant Upper Liassic, Triassic and Permian forms. This has involved a complete redescription of the majority of the Palaeoniscoid and Subholostean genera and of such Holosteans that have not previously been adequately described. The origins of the Holostei are investigated and it is concluded that they are of polyphyletic origin, at least three independently derived lines being recognizable within the group. The separate evolutionary lines within the Holostei are discussed and in particular that which leads through *Pholidophorus* to the Teleostei. A discussion is given of repeated parallel evolution within the various lines of Holostei.

I. INTRODUCTION

THERE are good modern accounts of a number of Triassic fish faunas. In the Lower Trias, marine faunas from Spitsbergen, Greenland and Madagascar have been described by Stensiö (1921, 1925, 1932) and Piveteau (1934, 1941), and freshwater faunas from Australia by Wade (1935, 1940, 1941). In addition, there are more recent accounts of faunas from the Lower Trias of Madagascar by Lehman (1952), from the Middle Trias of Besano, Lombardy by Brough (1939), and from the Lithographic Stone (Lower Kimmeridgian) of Cerin by Saint-Seine (1949). However, the rich fauna from the Lower Lias has received no modern comparable treatment.

The earliest descriptions go back to Egerton (1852) and were revised by Woodward at the end of the last century in the British Museum *Catalogue of Fossil Fishes*. More recently Rayner (1941, 1948) has redescribed several of the more important Holosteans and attempted a classification of the group.

England has produced the majority of the known fishes from the Lower Lias, Lyme Regis being by far the richest locality. Other localities include Watchett and Street, in Somerset; Stratford-on-Avon, Warwickshire; Barrow-on-Soar, Leicestershire; Bushley, Gloucestershire. Abroad, specimens come from Alsace-Lorraine, Würtemburg and a few other German localities. The main collection is in the British Museum (Natural History).

The fauna is large and well preserved. It includes Elasmobranchs, Chimaeroids, Sturgeons, Coelacanths, Palaeoniscoids, Subholosteans, and many Holosteans, which last form the bulk of the collections. The limy matrix in which the specimens are preserved makes possible the application of the modern technique of acid preparation (Toombs 1948; Rixon 1949).

The fauna is important as it throws light both on the origin of the Holostei and on the evolution, from the Holostei, of the present day Teleosts.

II. SYSTEMATIC DESCRIPTION

Order *PALAEONISCOIDEA*

Family Coccolepidae

Diagnosis. Palaeoniscoid fishes of slender fusiform shape with deeply forked, somewhat unequilobate tails. Fins of Palaeoniscid type, large, with the rays all articulated and branching distally; lepidotrichia far more numerous than supporting radials. Mandibular suspensorium oblique, dentition consisting of a set of regularly spaced, large teeth, interspersed with minute, sharply pointed teeth. Branchiostegal rays well developed. External skull bones generally ornamented with irregular tubercles and ridges. Fulcra minute or absent. Scales thin and deeply imbricating, ornamented with tubercles of enamel.

Genus ***COCCOLEPIS*** Agassiz, 1843

Diagnosis. As for family (only genus).

Type species. *Coccolepis bucklandi* Agassiz.

Remarks. The genus *Coccolepis* was founded by Agassiz (1843: 300, pl. 36, figs. 6, 7) when he described *Coccolepis bucklandi*. Since that date eight other members of the genus have been described, *Coccolepis andrewsi, liassica, australis, macroptera, aniscowitchi, martynovi, cockerelli* and *socialis*, although Berg (1948: 1243) considers both *C. socialis* and *C. cockerelli* to be synonymous with *C. aniscowitchi*. However, although the obvious Palaeoniscid affinities of the genus were recognized at an early date, there has been no adequate description of any of the individual species. With this in mind I have undertaken a re-examination of the species *Coccolepis liassica*.

Coccolepis liassica Woodward

(Text-figs. 1, 2, 4)

1890. *Coccolepis liassica* Woodward, p. 432, pl. 16, figs. 2–4.
1891. *Coccolepis liassica* Woodward : Woodward, p. 525.

DIAGNOSIS. A *Coccolepis* of moderate size, length of head contained about four and a half times in total length and equals the maximum depth of body. External skull bones strongly ornamented with rounded tubercles and a few ridges. Subopercular deeper than broad, larger than the opercular.

SYNTYPES. B.M.N.H. P 887, P 6153 and 39865 from the Lower Lias, Lyme Regis.

MATERIAL. Specimens in the B.M.N.H.

DESCRIPTION. *The skull.* The general shape of the skull can be seen from Text-fig. 1. The snout is rounded with the orbit lying well forward. The relatively large nasal orifice is situated more ventrally than in the majority of Palaeoniscids. The external bones of the skull are all ornamented with enamel, and so in life were not covered by soft tissues. The ornamentation of the skull roofing bones consists of pronounced coarse tubercles, which in places give way to a more rugose structure. A similar somewhat finer ornamentation covers the nasal, postrostral and preopercular. The maxilla is characterized by lines of tubercles which occasionally anastomose into ridges. The supraorbital and infraorbital bones have barely any

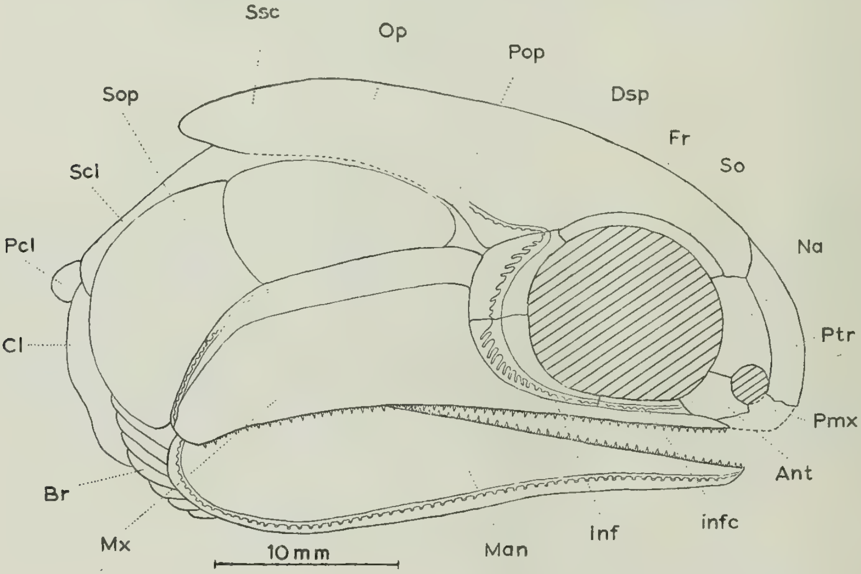


FIG. 1. *Coccolepis liassica* Woodward. Restoration of skull in lateral view.

ornamentation. The ornamentation of the opercular and the subopercular shows numerous coarse striae which run concentrically around the bones, whilst the branchiostegal rays also exhibit similar concentric striations. The mandible is much more coarsely ornamented than the skull bones, and has a pronounced mandibular sensory canal running along its length. The passage of this canal is marked by a series of pits which open to the exterior.

All the specimens of *Coccolepis liassica* are laterally crushed and consequently the demarcation of the individual skull roofing bones is difficult to interpret. Only in the anterior region can suture lines be made out with any degree of certainty. The frontals constitute the major portion of the skull roof, and anteriorly they meet the postrostral and nasals. The postrostral is a large bone whose general shape can be seen in B.M.N.H. P 11772. It extends downwards to form the rostrum and on either side it joins the nasal along most of its length. Posteriorly the nasal borders a considerable portion of the orbit ; dorsally it abuts against the supraorbital and ventrally the antorbital. In its antero-ventral corner the nasal has a pronounced semicircular notch, this forms part of the border of the nasal orifice. The antorbital is of a roughly triangular shape and limits the orbit behind and the nasal orifice in front. No trace of a premaxilla could be found, but from the general shape of the bones in the anterior region there is reason to believe one existed. It must have adjoined the antorbital and the maxilla posteriorly and the postrostral dorsally. The other bones limiting the orbit are the infraorbitals beneath and behind and the supraorbital above. The most anterior infraorbital is a narrow bone extending back along the dorsal margin of the maxilla from the antorbital to the next infraorbital. The second infraorbital is narrow anteriorly, but as it extends upwards it broadens considerably. From the infraorbital a broad dermosphenotic limits the remainder of the posterior edge of the orbit. The dermosphenotic is connected to the infraorbital by a straight suture and ventrally rests in the concave anterior margin of the maxilla and the preopercular. Running through the surface of the dermosphenotic and the infraorbitals is the intraorbital sensory canal. As this canal traverses the dermosphenotic and the succeeding infraorbitals it gives off numerous fine branches posteriorly. These can be seen on B.M.N.H. P 11772. Along the lateral edge of the frontal and bordering the orbit above is the single supraorbital bone.

The maxilla is of the normal Palaeoniscid pattern, much broadened posteriorly and long and slender anteriorly. Its oral border is completely lined with teeth, right back to its extreme posterior angle. The teeth are in two series, the larger, regularly spaced, slender and slightly curved teeth interspersed with minute, sharply pointed teeth. The preopercular is very much smaller than the maxilla, to which it is attached along the whole of its length, forming almost a cap to the latter bone. The preopercular sensory canal can be traced part of the way along its posterior border. The suspensorium is very oblique, as can be observed from the angle of the opercular bones. The opercular itself lies almost horizontal above the dorsal edge of the preopercular. There is no evidence of any other bones between these two elements corresponding to the " dermohyal " of Moy-Thomas & Dyne (1938 : 441) or to the bone " X " of Traquair (1901 : 83). The subopercular is more vertical in position, deeper than broad and larger than the opercular. There are fifteen branchiostegal rays on each side, broadened anteriorly and delicately ornamented with concentric striations. The gular plate is relatively small in this species and it is similarly ornamented to the branchiostegal rays. The lower jaws are stout and bear numerous teeth along their posterior margins. The dentition is similar to that of the maxilla with two series present. The teeth of the larger series are somewhat stouter than the corresponding ones found in the maxilla. Of the other skull bones little can be made out.

Appendicular skeleton. The pectoral girdle is not complete in any of the specimens, but its general form can still be ascertained. The supracleithrum is a wide bone stretching from the expanded suprascapular to midway down the subopercular. Here it joins a somewhat reduced cleithrum. A small almost circular postcleithrum is also present. The fin itself is small with between eighteen and twenty lepidotrichia. The rays are distally dichotomized and distantly articulated. The fin has a narrow insertion and there are no fulcral scales present.

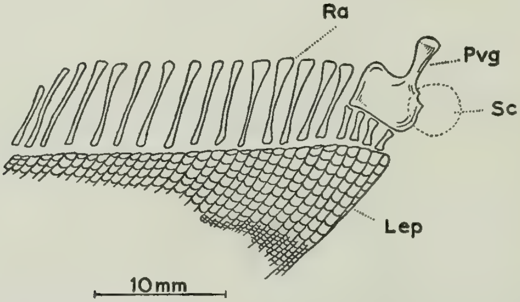


FIG. 2. *Coccolepis liassica* Woodward. Girdle and supporting structures of the pelvic fin. From B.M.N.H. P 3697 and P 894.

The structure of the pelvic fins and girdle can be seen on B.M.N.H. P 894 and its counterpart P 3697 (Text-fig. 2). Internally there is a paired skeletal structure of rather unusual form, consisting of an almost square plate with a projection from its antero-dorsal corner. This projection meets that of its opposite member to constitute the pelvic girdle. Immediately below this paired structure are four reduced radials and posterior to it another fifteen longer radials, making nineteen in all. From the radials arise twenty-nine lepidotrichia which make up the pelvic fin. The base line of this fin is extended and the fin arises slightly to the anterior of the dorsal fin, midway between the pectoral and anal fins. The fin is triangular in outline, with all the rays articulated and branching distally.

Unpaired fins. The dorsal fin (Text-fig. 3) arises at the middle point of the back opposite the posterior half of the pelvic fin. The fin is distinctly triangular, similar in outline to the anal, but with a shorter base. There are between twenty and twenty-five lepidotrichia, which increase in length up to the fifth, and then decrease in length as they pass backwards. A typical diamond-shaped fulcral scale was observed at the anterior end of this fin, in contrast to the statements to the contrary by previous workers (Woodward, 1891 : 523). Supporting the dorsal fin is a series of endoskeletal supports, but since the material was poorly preserved in this region, examination of another species was necessary to obtain a clear picture. A specimen of *Coccolepis andrewsi* (B.M.N.H. P 6302) shows a beautifully preserved dorsal fin, from which I have drawn Text-fig. 3. There are approximately nineteen of these endoskeletal supports, long and rod-like in general shape and expanded at their articulation with the fin rays (numbering twenty-nine to thirty in *Coccolepis liassica*). Beneath these endoskeletal supports the neural arches are reduced, the neural spines being absent.

The anal fin (Text-fig. 4) is similar to the dorsal with twenty-five lepidotrichia all distally dichotomized. There are between twelve and thirteen endoskeletal rods supporting the fin (B.M.N.H. P 11772). They are of the same general shape as those of the dorsal, perhaps a little more expanded at their articulatory points with the fin rays.

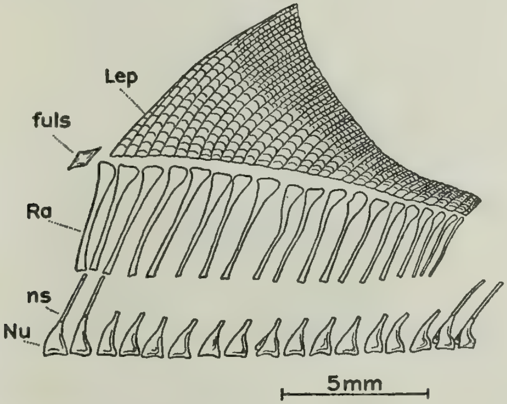


FIG. 3. *Coccolepis andrewsi* Woodward. Reconstruction of dorsal fin. From B.M.N.H. P 6302.

The heterocercal tail is deeply cleft with the upper lobe slightly the longer. There appear to be about forty-one fin rays of which the principal rays of the lower lobe are the stoutest. The fulcral ridge scales are well developed along the upper lobe of the tail, being arranged in six to seven rows with approximately twelve scales in each row.

Axial skeleton. The notochord was persistent since there are no traces of ossification in the notochordal sheath. The neural and haemal arches which bound the space occupied by the persistent notochord, are present along the whole length of the fish. The neural arches anterior to the dorsal fin bear long neural spines, which are not fused to the supporting arches, but remain quite distinct. These spines are missing in the area of the dorsal fins, but more posteriorly in the caudal region they are again present, although fused completely with the rest of the neural arch. Anteriorly the haemal arches are much reduced, bearing no spines. The arches become stouter in the caudal region (just anterior to the anal fin) and have long haemal spines. The most posterior haemal arches are elongated and distally thickened for the articulation of fin rays in the lower lobe, whilst the upper lobe rests on a series of slender rods which are in all probability neural spines.

Squamation. Very few of the specimens exhibit scales, but one or two isolated flank scales are visible on P 4370*a*. These scales are cycloidal in form and each divided into two distinct areas. The more anterior, overlapped portion is ornamented by fine concentric lines, but the ornamentation of the exposed area is more elaborate, consisting of lines of tubercles horizontally arranged with occasionally some of the tubercules fusing into ridges. There appear to be fulcral scales only in front of the dorsal fin (one ridge scale being recognized) and on the upper caudal lobe. Here the scales are more diamond-shaped, smooth and arranged in six to seven rows along the length of the lobe.

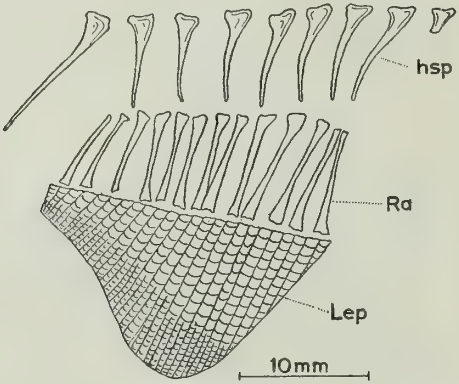


FIG. 4. *Coccolepis liassica* Woodward. Reconstruction of anal fin, mainly from B.M.N.H. P 11772.

Family CENTROLEPIDAE

DIAGNOSIS. Palaeoniscoid fishes of moderate size, fusiform shape and elongate bodies, with the maximum depth of the trunk equalling the length of the head, and contained almost four times in the total length. Opercular twice as long as broad, and a little larger than the preopercular. Two suborbitals present. Fins large and of the Palaeoniscoid type, with stout, flattened rays, all articulated and distally bifurcating ; anteriorly fringed with well-developed fulcra. Mandibular suspensorium oblique, dentition consisting of an inner series of large, widely spaced teeth, an outer series of more closely set, much smaller and sharply pointed teeth, and a shagreen of small rounded denticles on the coronoid, palate and branchial apparatus. External skull bones ornamented with tubercles and ridges of enamel. Form of the tail unknown. Scales thick and highly ornamented with serrations, ridges and furrows.

Genus **CENTROLEPIS** Egerton, 1858

Diagnosis. As for family (only genus).

Type species. *Centrolepis aspera* Egerton.

Remarks. The genus *Centrolepis* contains only one species, *Centrolepis aspera.* Woodward (1891 : 521) classified it with the Palaeoniscids, mainly on the character of the skull roofing bones. Later Romer (1945 : 580) placed *Centrolepis* under the heading Palaeoniscoidea or Subholostei *Incertae Sedis.* It is shown below that the genus correctly belongs with the Palaeoniscoidea as Woodward (1891) anticipated.

Centrolepis aspera Egerton

(Text-figs. 5–12)

1844. *Centrolepis aspera* Agassiz, **2**, pt. 1, p. 304.
1858. *Centrolepis aspera* Egerton, no. 5, pl. 5.
1890. *Centrolepis aspera* Egerton : Woodward, p. 430, pl. 16, fig. 1.
1891. *Centrolepis aspera* Egerton : Woodward, p. 521.

Diagnosis. As for family and genus (only species).

Holotype. A well-preserved laterally crushed specimen in the B.M.N.H., represented by P 582 and the counterpart P 3510. Lower Lias, Lyme Regis.

Material. Specimens in the B.M.N.H.

Description. *The skull.* The skull of *Centrolepis* is long, with a very oblique suspensorium and the orbit situated well forward (Text-fig. 5). The suprascapulars, frontals and parietals are covered with small symmetrically placed tubercles of enamel, which on the nasals and postrostral give way to raised ridges of enamel which run along the length of the bones. The small portions of the infraorbital series (B.M.N.H. 38123) which can be distinguished show a tubercular pattern, whilst the two members of the suborbital series have ridges of dentine similar to those of the nasals. The maxilla exhibits vertical striae near its ventral border, but these soon break up into separate tubercles so that the major portion of this bone and the preopercular have an ornamentation similar to that of the roofing bones. The ornamentation of the opercular is somewhat different, consisting of rows of tubercles running along its length with distinct grooves in between the separate rows. A similar pattern is to be found on the subopercular, but here the rows and grooves run more concentrically round the bone. The branchiostegal rays are coarsely tuberculated, while on the mandible stout ridges or striae run more or less along its length.

The few specimens belonging to this species are all laterally crushed, thereby making the interpretation of the skull roofing bones very difficult. The posterior extremity of the skull is covered by a distinct suprascapular from beneath which appears the large supracleithrum. The parietals and frontals are both large and constitute the major portion of the skull roof with the dermopterotics considerably extending its lateral borders. Anteriorly the frontals meet the nasals and postrostral. The postrostral abuts on the nasal along its entire posterior edge except where the external nares occur. The postrostral forms the anterior edge of the orifice and the nasal the posterior, much as in many of the Palaeoniscoids described by Moy-Thomas & Dyne (1938). Posteriorly the nasal borders the orbit and dorsally articulates with the frontal and supraorbital. Ventrally it joins the rostralo-premaxillary. From B.M.N.H. P 5594 the internal structure of the nasal and the postrostral can be seen (Text-fig. 6). On the inner surface just posterior to the nostril there is a bridge of bone on the wall of the nasal, a structure of which there is no previous account in the literature. It is obviously part of the nasal passage but its significance is not apparent. Also, on the inner surface a series of circular pits occurs in the bone (Text-fig. 6). The main infraorbital sensory canal round the snout does not split into two branches while in the rostral-premaxillary, as in most of Moy-Thomas & Dyne's illustrations (1938), but divides into two in the nasal, the main branch continuing up round the nasal and on to the frontal, while the smaller branch passes into the postrostral. It seems probable that the bone I have termed nasal represents two elements, the nasal and the antorbital which have become fused. The rostralo-premaxillary, the internal surface of which can also be seen on P 5594, articulates with the nasal dorsally, the infraorbital posteriorly and the maxilla ventrally. It forms a small portion of the border of the orbit and does not appear to bear any teeth. The infraorbital series comprises two bones which border both the lower rim

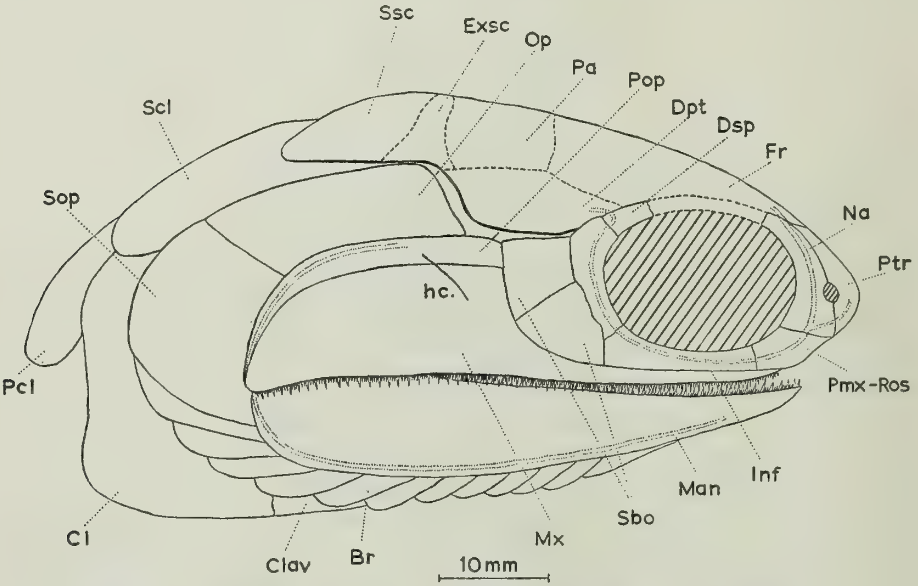


FIG. 5. *Centrolepis aspera* Egerton. Reconstruction of skull in lateral view.

of the orbit and its posterior edge. The first member of the pair passes back from the rostralo-premaxillary with its ventral edge in contact with the maxilla. Posteriorly it abuts the suborbital and the other infraorbital. The second infraorbital passes upwards articulating with the anterior edges of the two suborbitals. Dorsally it adjoins a small fragment of bone (see 38123) which represents part of the dermosphenotic. The infraorbital sensory canal can be traced from the dermopterotic, into the dermosphenotic, where it turns sharply downwards and passes round through the infraorbitals into the rostralo-premaxillary. The two suborbitals are largish bones which fit in between the infraorbitals and the concave anterior edge of the maxilla and preopercular. The maxilla and preopercular are typically Palaeoniscid in structure. The maxilla is much broadened posteriorly and is long and slender anteriorly. The oral border of the maxilla bears teeth along its entire length, the teeth being in two series, an outermost series of small, numerous, sharply pointed teeth, and an inner series of much larger, less numerous and slightly curved teeth. The preopercular sensory canal runs along the posterior border of the preopercular, and the supramaxillary canal is represented by a distinct groove which passes from the antero-dorsal region of the preopercular down into the maxilla (*hc.* in Text-fig. 5).

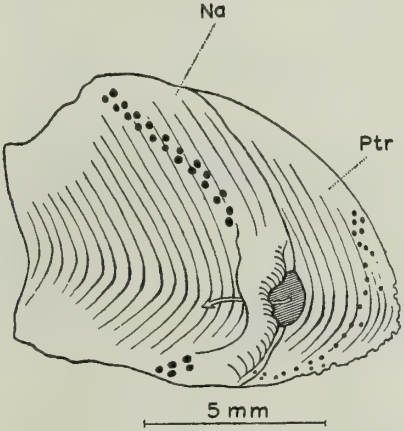


FIG. 6. *Centrolepis aspera* Egerton. Nasal and postrostral bones of the left side showing internal nares. From B.M.N.H. P 5594.

From the angle of the opercular bones the suspensorium is very oblique, with the opercular lying almost horizontal above the preopercular. The opercular is almost twice as long as it is broad and is a little larger than the subopercular. The subopercular is more vertical in position and as broad as it is deep. The number of branchiostegal rays that can be counted with any accuracy is twelve, although this is probably a little less than the correct number.

Lower jaw. The bones of the lower jaw are well preserved in P 5594 (Text-fig. 7). The greater portion of the jaw is made up of the dentary. The surangular is small and forms a neat socket for the articulatory surface of the upper jaw. The remainder of the posterior edge of the jaw is made up of the angular. This bone does not seem to pass very far forwards, but since the inner surface of the jaw is not exposed its true extent cannot be determined. The dentary overlaps the angular and the surangular. Dorsally the dentary has a series of teeth on it. These teeth are of two sizes, much as in the maxilla, the outermost series being more closely set, of medium height, thin and sharply pointed (t_1), whilst labial to these is a series of much larger widely spaced teeth (t_2). Both sets of teeth are on the edge of a shelf which is formed by a continuous coronoid. The coronoid on its lingual surface bears a series of large tubercles (t_3), much larger than the shagreen of small rounded denticles on the palate and branchial apparatus.

Palate. The structure of the palate of *Centrolepis* is shown on the same specimen P 5594 (Text-fig. 8). Here practically the whole of the palate is visible with the exception of the posterior end, which is somewhat obscured by the hyomandibular and parts of the branchial apparatus. The suprapterygoid series is represented by one bone only, which runs the whole length of the dorsal border of the palate. This single suprapterygoid is expanded posteriorly where it joins the metapterygoid and pterygoid, but becomes much reduced as it continues forwards. Anteriorly the suprapterygoid broadens again slightly. Posteriorly beneath the suprapterygoid and between it and the ectopterygoid, is a small metapterygoid. The suture line between the metapterygoid and the pterygoid is rather indistinct, but by examination under xylol and carbon tetrachloride it could be discerned. The ectopterygoid, which forms the postero-ventral portion of the palate, bears a single row of large tubercular teeth on its lateral margin, and this row is continued forward on to the palatine. The rest of the palate is made up of the large pterygoid which passes forward and ends rather bluntly. The pterygoid extends from the ethmoid region backwards to terminate some distance in advance of the quadrate, between the metapterygoid

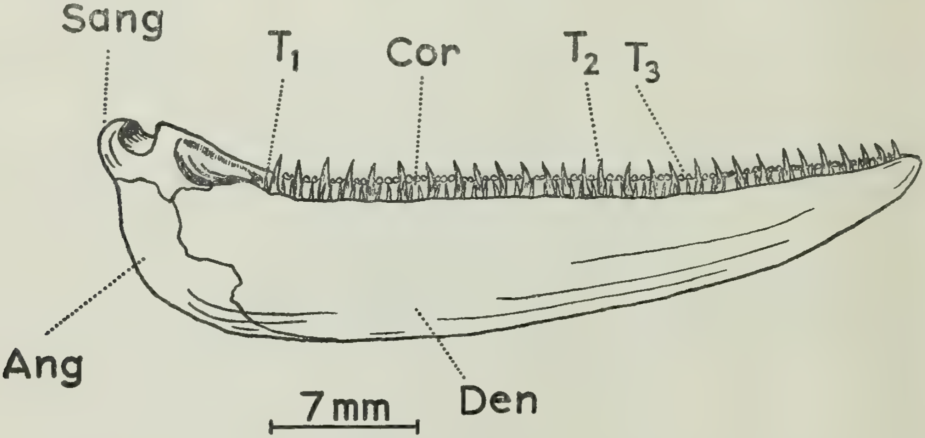


FIG. 7. *Centrolepis aspera* Egerton. Lower jaw, from B.M.N.H. P 5594, dentition from B.M.N.H. P 38123.

and the ectopterygoid. The palatine is represented by a narrow strip of bone lying between the lower border of the pterygoid and the maxilla.

Hyobranchial apparatus. This too can be seen in specimen P 5594 where it has been a little distorted and crushed during fossilization (Text-fig. 9). The hyomandibular is represented by a thin rod of bone somewhat expanded dorsally to become blade-shaped. It overlies the upper border of the suprapterygoid, but its connection with the quadrate cannot be seen. No trace of the ceratohyals can be found, although both hypohyals are present. The hypohyal is a stout ossification, with a V-shaped posterior border. This is articulated with a conical almost pointed basihyal. Behind the basihyal are two median basibranchials similar to those described by Watson (1925 : 863) for *Elonichthys aitkeni*. The first and second branchial arches have long hypobranchials, those of the third and fourth being slightly shorter. The four ceratobranchials are slender and the first two are only partly preserved in this specimen. The fourth ceratobranchial is the most complete and has a small protuberance facing posteriorly near its dorsal extremity. The basihyals, hypohyals and basibranchials are all covered with a shagreen of fine denticles and traces of this also appear on the hypobranchials. It is probable that the whole branchial apparatus was covered with such denticles.

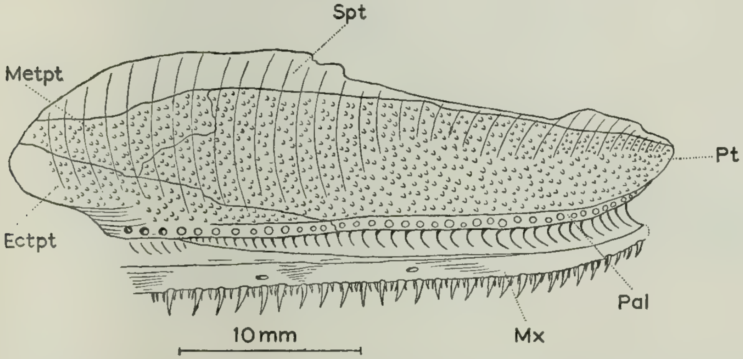
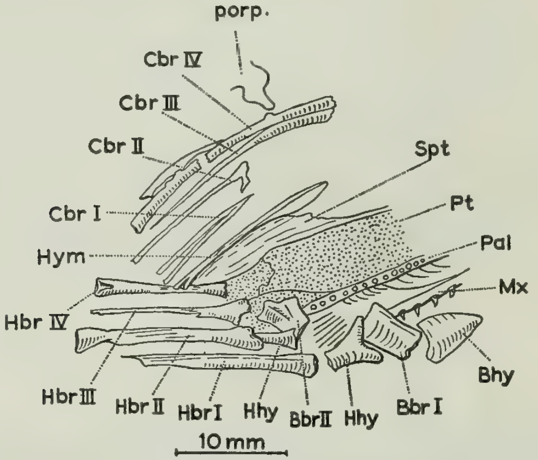


FIG. 8. *Centrolepis aspera* Egerton. Left side of palate viewed from its admesial surface, mainly from B.M.N.H. P 5594.

Appendicular skeleton. The supracleithrum is very long and extends down from the suprascapular to well beyond the junction of the opercular and subopercular (Text-fig. 5). It is ornamented with coarse tubercles similar to the patterning found on the skull roofing bones. The postcleithrum is also long—about half the length of the supracleithrum—with similar ornamentation, except near its posterior edge where the tubercles fuse into striae.

The cleithrum is both deep and robust, heavily ornamented with tubercles and ridges, especially posteriorly (Text-fig. 10). The antero-dorsal margin is distinctly concave and helps to form the posterior boundary of the gill chamber. The convexity in its lower posterior margin on the other hand is less pronounced. The clavicle is another stout ossification and posteriorly overlaps the end of the cleithrum (in P 5594 it has been displaced). In profile the clavicle is approximately triangular, and has a well-marked foramen (*f*) running through it. In describing the pectoral girdle of the Palaeoniscoid *Acrorhabdus bertili*, Stensiö (1921 : 229) figures a nerve canal running through the primary girdle plate. Since this foramen in the clavicle of *Centrolepis* would be in a direct line with such a nerve canal I think it more reasonable to suppose it transmitted nerves rather than blood vessels.


porp.
Cbr IV
Cbr III
Cbr II
Spt
Cbr I
Pt
Pal
Hym
Mx
Hbr IV
Bhy
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HbrII
HbrI
Hhy
BbrII
Hhy
BbrI
10 mm

FIG. 9. *Centrolepis aspera* Egerton. Hyobranchial apparatus, left side. From B.M.N.H. P 5594.

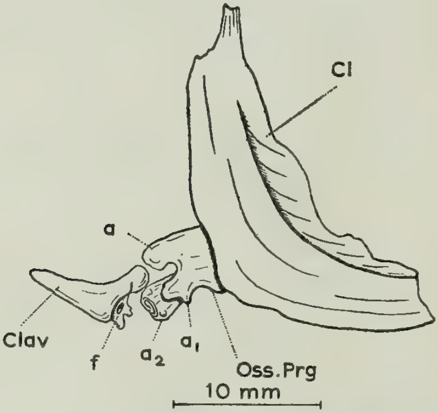

Cl
a
Clav
f
a2
a1
Oss.Prg
10 mm

FIG. 10. *Centrolepis aspera* Egerton. Cleithrum, clavicle and primary girdle, from B.M.N.H. P 5594.

A primary girdle plate is present in this specimen and projects from beneath the postero-ventral margin of the cleithrum (Text-fig. 10). The outermost portion is a thin plate produced into two blunt processes (*a* and a_1) which face posteriorly. Beneath it and a little deeper is a stouter portion pointing backwards and downwards (a_2). No radials or lepidotrichia are visible.

The structure of the pectoral fin on 38123 shows it to possess between twenty-five and thirty stout lepidotrichia. The pelvic fin has between thirty and thirty-five and the anal much fewer, between fifteen and twenty.

Unpaired fins. The dorsal fin is quite long-based, with thirty to thirty-five lepidotrichia. The dorsal and anal fins are triangular in shape, the dorsal opposed to the space between the pelvic fins and the anal. Nothing further of the axial skeleton can be made out on any of the other specimens.

Squamation. The scales are thick, of moderate size and highly ornamented. In the abdominal region the scales have ridges and denticles which run along their length, but in the anterior region of the scale the ridges run vertically. In the caudal area the scales are coarsely serrated posteriorly, with a few short ridges anteriorly.

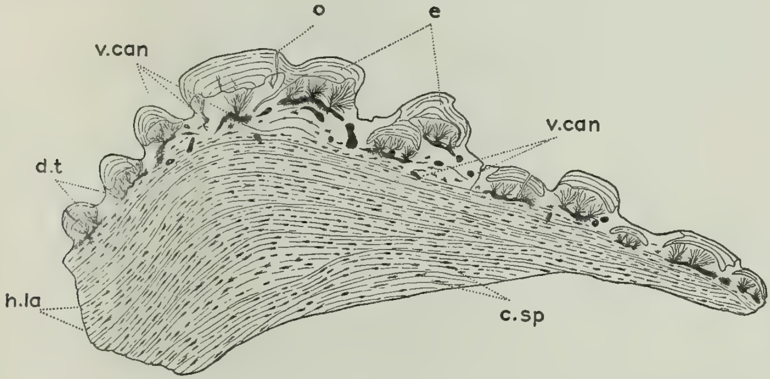


FIG. 11. *Centrolepis aspera* Egerton. Oblique section of scale, B.M.N.H. 11260, much enlarged.

From a microscopic examination the scales are obviously similar to the " Palaeoniscoid " scale of Goodrich (1907) and agree closely with the structure of scales of other Palaeonisciformes described by Ørvig (1957).

The scales (Text-figs. 11, 12) are made up of a superficial layer of enamel (*e*) and dentine, with a basal portion of laminar bone (*h. la.*). Beneath the enamel, which is often raised up into ridges and tuberculations, is a horizontal network of canals (*v.can.*). Occasionally from this network a vertical canal arises and pierces the surface of the enamel (*o*). Also from this horizontal network arises a system of long upwardly directed dentinal tubules (*d.t.*). Beneath the horizontal canal system the laminar bone occurs, showing the primitive condition where the bone tissue contains cell spaces throughout its length (Text-fig. 11). These cell spaces (*c.sp.*) are more or less horizontally arranged and follow the course of bone lamellae. This basal bone is penetrated by numerous thin vascular canals of Williamson (*can.W.*). These canals run somewhat obliquely upwards from the basal portion of the scale. The canals are thin and of characteristic shape much as in *Orvikuina* (Ørvig, 1957, fig. 3), possessing short ramified side twigs (*s.br.*). Unlike *Orvikuina* they do not contain the cells which gave rise to the bone lamellae, instead these cells are arranged between the canals of Williamson. Their distribution here is random, and there is no concentration around the canals.

In general perspective the scale of *Centrolepis* appears primitive and shows little specialization, the canals of Williamson still appearing to retain their vascular function, the bone cells being randomly arranged, the dentine layer is still present, and the whole scale is capped with a layer of enamel.

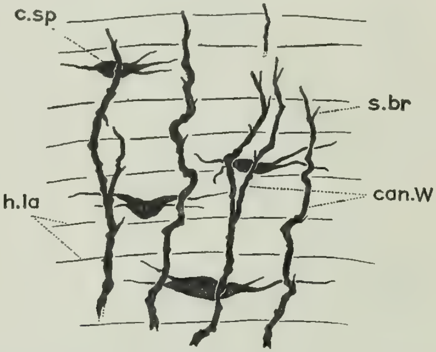


FIG. 12. *Centrolepis aspera* Egerton. Vertical section of the basal bone tissue of the scale. ×250 approx. B.M.N.H. 11260.

"*SUBHOLOSTEI*"

Family PLATYSIAGIDAE

DIAGNOSIS. Subholostean fishes of elongate-fusiform shape with deeply forked equilobate tails. Paired fins Holostean in structure and of moderate size. Fins have numerous small fulcra, the lepidotrichia are stout and bifurcated and all articulated distally. The mandible has a broad coronoid process, the dentition consists of a series of large, conical, pointed teeth, interspersed with numerous, irregularly arranged smaller teeth. The maxilla is Palaeoniscid in make-up, but the preopercular is much expanded and the suspensorium upright. Branchiostegal rays well developed. External skull bones heavily ornamented, with tubercles and ridges. Scales thin, rhombic, covered with enamel and ornamented with feeble ridges and a few scattered tubercles anteriorly. The posterior margins of the scales are denticulated.

Genus ***PLATYSIAGUM*** Egerton, 1872

DIAGNOSIS. As for family (only genus).

TYPE SPECIES. *Platysiagum sclerocephalum* Egerton.

REMARKS. The genus contains two species, *Platysiagum sclerocephalum* Egerton from the Lower Lias of Lyme Regis, and *Platysiagum minus* Brough from the Middle Trias of Besano.

The genus was first described by Egerton (1872 : no. 6, pl. 6) as belonging to the order Ganoidei and to the heterogeneous family the Sauroidei. Later Woodward (1895*b* : 532) included it in the Palaeoniscidae. He was of the opinion that the arrangement of the cheek plates alone was sufficient for determining the systematic position of the genus.

It was not until 1939 that Brough (p. 18) recognized the genus as being more Holostean in affinities than Palaeoniscoid. His conclusions were substantiated by the discovery of the second species, *Platysiagum minus*, in the fauna collected from Besano. This species had somewhat better preserved fins than are found in any of the existing specimens of *Platysiagum sclerocephalum*, and from the nature of the paired fins (which are distinctly Holostean), the hemiheterocercal tail and the incipient interopercular, Brough concluded that the genus was at the Subholostean level of evolution.

Platysiagum sclerocephalum Egerton

(Text–fig. 13)

1872. *Platysiagum sclerocephalum* Egerton, no. 6, pl. 6.
1895*b*. *Platysiagum sclerocephalum* Egerton : Woodward, p. 533.
1939. *Platysiagum sclerocephalum* Egerton : Brough, p. 17.

DIAGNOSIS. A *Platysiagum* comprising fishes of moderate to large size. Length of head much exceeding the maximum depth of the trunk. Tuberculations on scales sparse.

SYNTYPES. B.M.N.H. P 3650, P 1333 and P 558, from the Lower Lias, Lyme Regis.

MATERIAL. Specimens in the B.M.N.H. and the Geological Survey Museum.

DESCRIPTION. *The skull.* In shape the head must have been quite blunt, and rounded anteriorly (Text-fig. 13). The external bones of the skull are stout and presumably articulated closely with one another. The ornamentation varies in character according to the position of the bone. Thus the bones constituting the top of the head are heavily ornamented with series of tubercles and ridges, which are especially prominent on the frontals. On the cheek bones the ridges are less frequent and the ornamentation generally less coarse. The opercular bones have only a slight ornamentation of small tubercles anteriorly, with an almost smooth posterior portion. Contrary to Woodward's statement (1895*b* : 533), the branchiostegal rays and gular plate are well ornamented. On a specimen in the Geological Survey Museum (G.S. 94743) the former can be seen to be ornamented with a fine, almost regular series of smaller tubercles. The pattern of ornamentation of the lower jaw is more coarse, very similar to that found on the frontals.

Very little can be made out of the bones of the skull roof. The major portion seems to have been formed by the frontals, but the extent of the other roofing bones is not clear. Posteriorly there appears to be a demarcation into suprascapulars and extrascapulars, but the limits of these cannot be defined with certainty. Passing forwards and downwards, the frontals abut on to the postrostral bone. Anterior to the postrostral is another bone, well shown in B.M.N.H. P 3650, occupying a medial position. This is the rostral bone, and it has a markedly rounded outline. The ornamentation of the rostral is rather remarkable, as it has a series of ridges running round it almost in half circles, reminiscent of the peculiar spiral ridges found on the postrostral of *Ptycholepis curta*.

The postrostral articulates laterally with the nasals, and with the rostral anteriorly. The premaxilla is a small ossification seen in B.M.N.H. P 3650, where it has three or four large teeth. The antorbital is a fairly large bone whose structure can be made out from B.M.N.H. P 3651. Antero-dorsally the antorbital articulates with the rostral bone, and in this region it is cut into by a pronounced semicircular notch, which can only be the nasal orifice. Ventrally part of one side of the antorbital abuts the maxilla, whilst more dorsally it articulates with the infraorbital. Anteriorly it joins the premaxilla. The dorso-posterior edge of the antorbital borders a small portion of the orbit. Posterior again to the antorbital and limiting the orbit behind and below is a series of two infraorbitals and a dermosphenotic. The first infraorbital is a slightly curved bone which broadens a little anteriorly to articulate with the

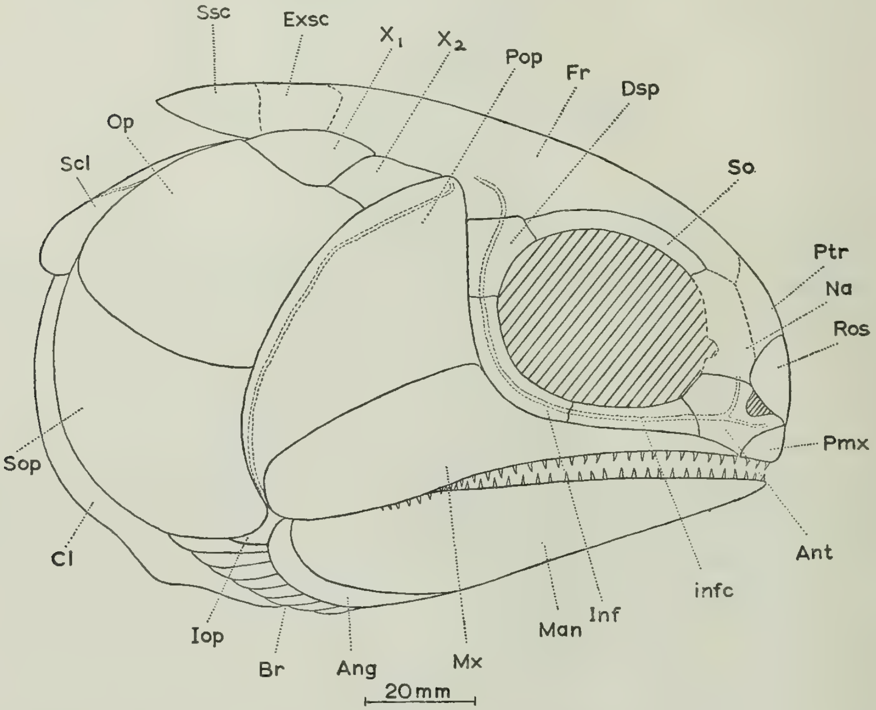


FIG. 13. *Platysiagum sclerocephalum* Egerton. Reconstruction of the right side of the head.

antorbital. Posteriorly it joins the second infraorbital which runs along part of the maxilla anteriorly, but passes backwards and upwards to border part of the preopercular as well. Above the infraorbital is a shorter stouter bone, the dermosphenotic. Dorsally the orbit is limited by a supraorbital bone, of much the same dimensions as the infraorbitals. Possibly this bone may have been made up of more than one element, but I was unable to ascertain this because of the poor state of preservation of the specimen.

The course of the sensory canals can be traced in places. The infraorbital canal is just visible in the dermopterotic, from where it runs through the dermosphenotic and on round the two infraorbitals into the antorbital. In the latter bone it branches into two, each branch passing to either side of the nasal orifice. The preopercular canal can be seen running through the postero-dorsal edge of the preopercular.

The major portion of the cheek is covered by two bones, the preopercular and the maxilla. The cheek region is characteristically of Palaeoniscoid form, apart from the very enlarged preopercular. The latter bone is a very large element, whose posterior edge describes a sweeping curve. This posterior margin is nothing like the straight edge found in *Platysiagum minus*. Along its entire length, the lower border of the preopercular is in very close contact with the maxilla. The maxilla is essentially Palaeoniscoid in pattern, with an enlarged rectangular posterior portion. Anteriorly it sweeps downwards and forwards, tapering almost to a point. Along its entire ventral length the maxilla bears teeth. The dentition consists of a series of large conical, sharply pointed teeth, interspersed with numerous irregularly arranged teeth.

The opercular cover consists of two principal plates of semicircular shape, the opercular and subopercular. The two plates are of approximately the same size, with rounded posterior margins. The effect is a continuous curved outline which runs down uninterrupted from the suprascapular to the first branchiostegal rays. Along the dorsal margin of the opercular lie two smaller bones, probably corresponding to Traquair's bone " X " (1901 : 83). They are members of the opercular series and not the preopercular series, since the preopercular sensory canal passes along the posterior border of the preopercular in such a position as would make it impossible for it to pass through either of the two bones. The more anterior of the pair, X_2, adjoins the preopercular. The interopercular is a small ossification, filling the gap between the end of the subopercular and the lower jaw.

There are eighteen to twenty branchiostegal rays on each side, and these are quite thin posteriorly, but increase in width anteriorly. The lower jaws are stout and bear numerous teeth along their posterior margins. The teeth are confined to a broad platform, and are similar to those found on the maxillae. Posteriorly this margin expands upwards into a large coronoid process. The bones of the lower jaw cannot be identified, but on B.M.N.H. P 558 the extent of the angular can be made out. This bone forms the most posterior margin of the jaw, but occupies only a small portion of its length. In front of the branchiostegal rays and between the jaw rami, a large ornamented gular plate is shown in G.S. 94743.

Of the other skull bones little remains. However, in specimen B.M.N.H. P 2046, the parasphenoid, pterygoid and ectopterygoid can be distinguished. The parasphenoid has a central area devoid of teeth, but on either side of this is a tooth series. In this series there are again two types of teeth, the larger, sharply pointed ones, and the smaller irregular teeth between them. The teeth are somewhat smaller than those found on the maxillae and mandibles. Alongside the parasphenoid are bits of the ectopterygoid and pterygoid ; these are covered by very fine granulations, or minute teeth.

Appendicular skeleton. The supracleithrum is a long bone much expanded ventrally, so that it is spatulate in shape. The ornamentation consists more of sculpturing than of tuberculations, giving it a pitted effect. The cleithrum is a relatively stout ossification with a distinct depression in it posteriorly for the reception of the pectoral fin. The ornamentation in this case is much more rugose with ridges rather than tubercles. The cleithrum is much broadened, and thicker ventrally. The pectoral fin consists of about twenty rays, with the anterior rays unjointed along most of their length. The first two rays anteriorly have a fringe of spiculae, but this is absent on the remainder. The fin insertion is constricted and narrow.

The pelvic fins have about twelve fin rays and again have a markedly constricted insertion. The general shape and structure of the paired fins is of distinctly Holostean form.

Unpaired fins. The dorsal fin consists of only a few stout rays, between ten and fifteen, but no evidence of an anal fin could be found on any of the specimens. Brough (1939 : 18) states that in *Platysiagum sclerocephalum* " the dorsal fin consists of about fourteen such rays ; those of the anal cannot be counted accurately ". Whatever he was looking at was certainly not an anal fin, since Woodward (1895*b* : 533) also failed to find any evidence of this fin.

The true structure of the caudal region is impossible to determine, but from Brough's (1939 : 17) notes on the species, and from his discovery in *Platysiagum minus* of a complete tail, it is probably correct to say that the tail in *Platysiagum sclerocephalum* was not completely heterocercal, but nearer the Holostean condition.

REMARKS. The genus *Platysiagum* is obviously of Palaeoniscoid origin. The characteristic maxilla still firmly united to a large preopercular as the essential cheek covering is most certainly a relic of its Palaeoniscoid ancestry. Higher members of the " Ganoid " grade have smaller, freed maxillae, and very much reduced preoperculae. However, the interopercular bone so characteristic of the Holostei is present in *Platysiagum sclerocephalum*, but a large opercular and subopercular still cover the gill chamber. The orbit is large and placed anteriorly, and has a complete set of infraorbital bones. In fact, the skull has departed little from the arrangement found in the Palaeoniscoidea.

The more advanced characters of the skull seem confined to the lower jaw where a coronoid process has developed and is overlapped by the posterior extremity of the maxilla. *Platysiagum* resembles the Semionotidae in its fusiform body and in the structure and distribution of its fins. This, together with the hemiheterocercal tail, the interopercular and the rhombic, ganoid scales, shows it to have progressed from the typical Palaeoniscoid make-up towards that found in the Holostei. This isolated genus was just another offshoot from the Palaeoniscoids, which had a short existence and eventually came to nothing.

Family PTYCHOLEPIDAE

DIAGNOSIS. Subholostean fishes, ranging from small to large size. Trunk elegantly fusiform and snout acutely pointed. Caudal fin deeply forked and hemiheterocercal. Suspensorium almost vertical, gape wide and orbit large. Dentition consisting of two series of small close-set teeth. Ornamentation of skull roofing bones distinct, with high ridges of enamel running more or less longitudinally.

The frontals are large and elongated, and constitute the major portion of the skull roof. The parietals are rectangular and much smaller. The elongated dermosphenotics border the frontals laterally, separating them from the orbit. The jaws are long, and the maxillae slender anteriorly. The maxilla is surmounted by a small triangular infraorbital.

The snout is covered by a large postrostral, bordered on either side by a pair of nasals. The opercular apparatus is somewhat quadrangular in shape, the opercular much deeper than wide and considerably larger than the subopercular. The first branchiostegal ray is much enlarged and there is a big gular plate in all species. There is no interopercular, and the pectoral girdle has a stout clavicle present.

The squamation is dense, scales thick, longer than wide and much elongated in the ventral region. The pectoral and pelvic fins well developed, dorsal and anal fins triangular, the former opposed to the pelvics, the latter small and remote. Fulcra conspicuous on all fins, biserial.

REMARKS. This family was originally associated with the Furidae (Woodward, 1895*b*: 316), but Brough (1939 : 17) and Aldinger (1937 : 276) have shown its affinities to be more with the Palaeoniscids and have traced its ancestry back to the Palaeoniscid *Boreosomus*.

Genus ***PTYCHOLEPIS*** Agassiz, 1833

DIAGNOSIS. As for family (only genus).

TYPE SPECIES. *Ptycholepis bollensis* Agassiz.

Ptycholepis monilifer Woodward

(Plates 36–40)

1895*b*. *Ptycholepis monilifer* Woodward, p. 322, pl. 10, figs. 2–4.

DIAGNOSIS. A *Ptycholepis* of large size, not less than 60 cm. in length. Ornamentation fine. Lepidotrichia ornamented with oblique ridges of enamel. Scales long and slender, with a few tubercles anteriorly, passing into long ridges which run downwards and backwards occasionally anastomosing.

HOLOTYPE. Fish in four pieces, B.M.N.H. 39868, from the Lower Lias, Lyme Regis.

REMARKS. The sole specimen of this species is 39868, from the Lower Lias of Lyme Regis. It is in four pieces, but, since these were collected at the same time and by a reliable collector, there is no reason to doubt that all four belong to one and the same specimen.

The only description is that given by Woodward (1895*b* : 322). A re-examination of this material has shown that Woodward has misinterpreted some of the bones, and since he figured only the lower jaw and a few scales, I am redescribing the species.

DESCRIPTION. On the first block (Pl. 36) there is a stout right mandibular ramus, very similar in shape and make-up to *Ptycholepis bollensis*. The jaw is 9·75 cm. in total length with a depth of approximately 2·4 cm. The alveolar border has a marked sigmoidal curvature, the highest point being 1 cm. anterior to the articulatory facet. There is a single series of small, robust, conical teeth. These teeth are markedly striated longitudinally around their bases, but have an almost smooth cap, reminiscent of the condition found in the Saurichthyids. The anterior extremity of the jaw tapers to a blunt point, where the ornamentation is coarser than over the remaining jaw surface. The ornamentation generally consists of superficial ridges, which although very irregular, pass upwards and forwards from the ventral margin. The ridges branch and interdigitate, but are nowhere near as coarse as those found on the lower jaw of *Ptycholepis bollensis*. Dorsally near the alveolar margin the ornamentation breaks up into isolated tubercles.

The surangular, a small bone bordering the articular facet, forms the most posterior portion of the jaw. The remainder of the posterior edge of the jaw is composed of the angular, which passes forwards and downwards from the anterior end of the articular facet. This bone also forms part of the lower border of the jaw, extending along almost half of its length. The bulk of the mandible is composed of the dentary, along which the course of the sensory canal is clearly marked by a series of pits. This mandibular canal finishes 5 mm. short of the anterior extremity of the jaw. Posteriorly the sensory canal can be traced back on to the angular, but its passage back up through the surangular is a little obscure. Lying above the jaw on the same block is a ceratohyal. It is fragmented anteriorly but the outline still remains on the underlying matrix. Posteriorly the bone ends bluntly, but passing forwards it narrows, and then broadens into an almost spatulate shape. Since this is the largest species of *Ptycholepis* the length of the ceratohyal can usefully be given as 5·45 cm.

On the second block (Pl. 37), the principal bone is the large right maxilla, incorrectly called a suboperculum by Woodward (1895*b* : 322). After a little development with needles, a set of teeth became apparent along its lower, somewhat concave border. These teeth are very similar in shape, size and pattern to those on the dentary. Occasionally the smooth cap has a semblance of striae on it. The maxilla is much longer than deep, over three times as long as its maximum depth. Its total length is 6·1 cm. after reconstruction, the outline of the posterior end, which is missing, being again easily seen on the underlying matrix. Dorsally it is overlain by the large first branchiostegal ray, but from the posterior extremity the maxilla sweeps forwards and upwards, then flattens out, and finally anteriorly it curves down again to form a short anterior process which bordered the lower rim of the orbit. Part of the anterior end of the maxilla has been broken off and is missing. Antero-dorsally the edge of the maxilla forms a narrow unornamented shelf, and on to this probably fitted an infraorbital series of bones. Elsewhere the maxilla is highly ornamented with ridges of enamel. These ridges follow the length of the bone, but posteriorly sweep round almost in contour fashion ; those in the dorsal region sweeping upwards, forming whorls of ridges, those in the ventral region sweeping downwards.

The bone on top of the maxilla, which Woodward (1895*b* : 322) called a large gular, is in fact this first enlarged branchiostegal ray. Then again, the bone which overlies the anterior extremity of the first branchiostegal ray is probably a member of the postorbital series. Both these last bones are practically smooth, but with the first branchiostegal ray having a small mesial area with a few isolated tubercles on it. On the same block there are ten other branchiostegal rays, very much narrower than the first, and all delicately ornamented with ridges and tubercles of enamel. Lying beneath the maxilla is a stout ossification, the homology of which it is almost impossible to decide. Rather tentatively I suggest that it is the crushed primary girdle element. Lying to the side of this is another indeterminate bone, which could be a clavicle.

The third block (Pl. 38) is much larger and contains the dorsal fin. The dorsal fin consists of about thirty lepidotrichia, with a few small slender rays anteriorly; these increase in length up to the seventh or eighth ray, and then progressively shorten as the fin passes backwards. No fulcra could be observed and the rays are undivided. All the rays were ornamented, especially near their bases. Anteriorly the ridges of enamel run diagonally across the stouter rays, but posteriorly the ridges run more parallel to the length of the rays.

Three of the body scales from this block have already been figured by Woodward (1895*b*, pl. 10, fig. 3). The scales are long and slender, with a few tubercles anteriorly passing into long ridges of enamel which run obliquely downwards and backwards (Pl. 40). These ridges sometimes branch and intercalate, but normally all terminate on the ventral border of the scale. The scales exhibit a delicate peg-and-socket articulation, not as strong as in *Lepidotes*, but again not really feeble as Woodward (1895*b* : 323) suggests. The peg is antero-dorsal in position being much nearer the anterior extremity, about a quarter of the way along its dorsal length. Also on this block is another large bone, with an ornamentation similar to that found on the maxilla. It is 6·5 cm. in length with its anterior margin produced into a sharp spur. The only bone with which it corresponds is the preopercular described in *Ptycholepis barboi* by Brough (1939, fig. 27). It is broader dorsally, with a distinct cleft, presumably for articulation with the dermopterotic. The posterior border is convex, whilst much of the outer surface of the bone is ornamented. The ornamentation is mainly in the form of ridges of enamel which sweep inwards from the posterior margin towards the spur. Dorsally there are a few tubercles and on either side of the spur the ridges form two whorls. Around the antero-dorsal cleft the bone is devoid of ornamentation, and again the spur and anterior edge of the bone are smooth. Running down the length of the bone is a distinct groove, this probably marks the course of the preopercular sensory canal, since in the dorsal region several distinct pits are visible.

Finally, the fourth block (Pl. 39) contains the caudal fin. This fin is large, 21 cm. from tip to tip, deeply cleft and strongly heterocercal. The lower lobe is somewhat the larger of the two, although the upper lobe was obviously produced, as is usual in this genus. The lepidotrichia are very numerous, stout anteriorly, but becoming very delicate and dichotomizing in their distal parts. The joints are stout proximally, but distally they are always longer than broad and often somewhat attenuated at the middle. The dorsal lobe has a double row of strong ridge scales along its dorsal edge. These scales are well developed and ornamented with tubercles and ridges of enamel.

Ptycholepis bollensis Agassiz

(Text-figs. 14–18)

1832. *Ptycholepis bollensis* Agassiz, p. 142 (name only).
1833. *Ptycholepis bollensis* Agassiz, **2**, pt. 1, p. 11.
1835. *Ptycholepis bollensis* Agassiz : Agassiz, **2**, pt. 2, p. 108, pl. 58*b*.
1849. *Ptycholepis bollensis* Agassiz : Williamson, p. 444.
1852. *Ptycholepis bollensis* Agassiz : Quenstedt, p. 203, pl. 15, fig. 5.
1856–58. *Ptycholepis bollensis* Agassiz : Quenstedt, pl. 30, figs. 1–7 ; pl. 31, fig. 8.
1865. *Ptycholepis bollensis* Agassiz : Cotteau, p. 337.
1875. *Ptycholepis bollensis* Agassiz : Sauvage, p. 8, pl. 2, fig. 2.
1891. *Ptycholepis bollensis* Agassiz : Sauvage, p. 33, pl. 1.
1895*b*. *Ptycholepis bollensis* Agassiz : Woodward, p. 317.
1896. *Ptycholepis bollensis* Agassiz : Woodward, p. 36, pl. 5.
1896. *Ptycholepis bollensis* Agassiz : Scupin, p. 169, pl. 10. fig. 5.
1919. *Ptycholepis bollensis* Agassiz : Hennig, p. 173.
1935. *Ptycholepis bollensis* Agassiz : Gross, pl. 7, fig. 2 ; text-figs. 27–29.
1937. *Ptycholepis bollensis* Agassiz : Aldinger, p. 286, text-figs. 85, 86*a*, 87*b*, 88*b*.
1952. *Ptycholepis bollensis* Agassiz : Hauff, p. 23, pls. 42, 43.

Diagnosis. A *Ptycholepis* of moderate size, attaining a length of some 35 cm. Body fusiform, deepened anteriorly. Orbit large, length of the head about a quarter of the total length of the fish and equals the maximum depth of the trunk.

Holotype. A much crushed and distorted fish, B.M.N.H. P 3688, from the Upper Lias of Whitby, Yorkshire.

Material. Specimens in the B.M.N.H., the Royal Scottish Museum, Edinburgh and the Tübingen Museum.

Remarks. This species was described by Agassiz (1835 : 108) and it is confined to the Upper Lias. Specimens come from the Upper Lias of Yorkshire, Germany and France.

Description. *The skull.* All the skull roofing bones are ornamented and patterned by deep grooves and ridges of enamel. These ridges are very coarse on the parietals, frontals, dermopterotics, suprascapulars, and dermosphenotics, where they run longitudinally along the length of the bones. The ridges run more obliquely on the extrascapular, and on the nasals they follow the sweep of the bone. Only the posterior half of the postrostral is ornamented by these parallel, longitudinal ridges ; the anterior half is completely smooth with its forward edge characteristically scalloped. The postorbital bones and the infraorbital show finer longitudinal ridges, but on the maxillae these ridges become broken up anteriorly into tubercles. The ornamentation of the opercular is more diffuse with ridges of enamel running more or less downwards in gentle curves from the antero-dorsal region (Text-fig. 14). The subopercular again shows longitudinal ridges, whilst the ornamentation on the mandible can be seen from Text-fig. 15. The first branchiostegal ray has a slight indication of ridging anteriorly, but the remaining rays and the median gular are comparatively smooth.

The character of the ornamentation of the skull roof makes the interpretation of the suture lines in that region difficult. However, one specimen of *Ptycholepis bollensis*, No. 10800, from the Upper Lias of Ohmden, Württemberg, in the Tübingen Museum, is flattened dorso-ventrally and shows the whole skull roof. From this specimen it was possible not only to work out the demarcation of the individual bones, but to trace the branches of the sensory canal system.

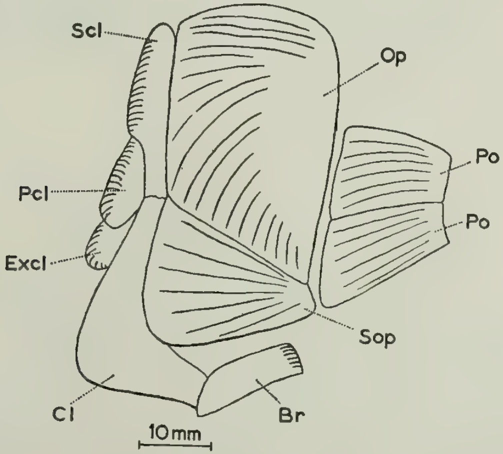


FIG. 14. *Ptycholepis bollensis* Agassiz. Sketch of a specimen from the Lias of Holzmaden, Germany, in the Tübingen Museum.

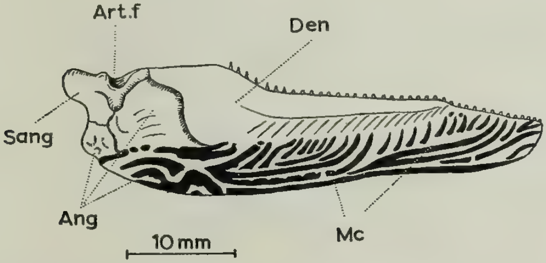


FIG. 15. *Ptycholepis bollensis* Agassiz. Lower jaw from B.M.N.H. P 3691*a*, dentition restored.

The major portion of the skull roof is made up of the large frontals (Text-figs. 16, 17). These are fairly narrow bones, broadened slightly near their centre. The suture between them is straight and does not interdigitate. Anteriorly the frontals end quite bluntly where they abut on to the postrostrals, and do not have the V-shaped insertion between the postrostral and nasals described by Brough (1939 : 68) in

Ptycholepis curta. Anteriorly the frontals border a small portion of the orbit. The parietals are about a third of the length of the frontals and are squarish in outline. Behind the parietals is a pair of extrascapulars. These, however, do not meet in the mid-line. Posteriorly to the extrascapulars, and a little below them, are the small suprascapulars.

Bordering the suprascapular and extrascapular anteriorly is a very large bone, the dermopterotic. This bone also borders the complete lateral edge of the parietal and part of the postero-lateral edge of the frontal. Abutting on the dermopterotic anteriorly and extending forwards is a long narrow ossification, the dermosphenotic.

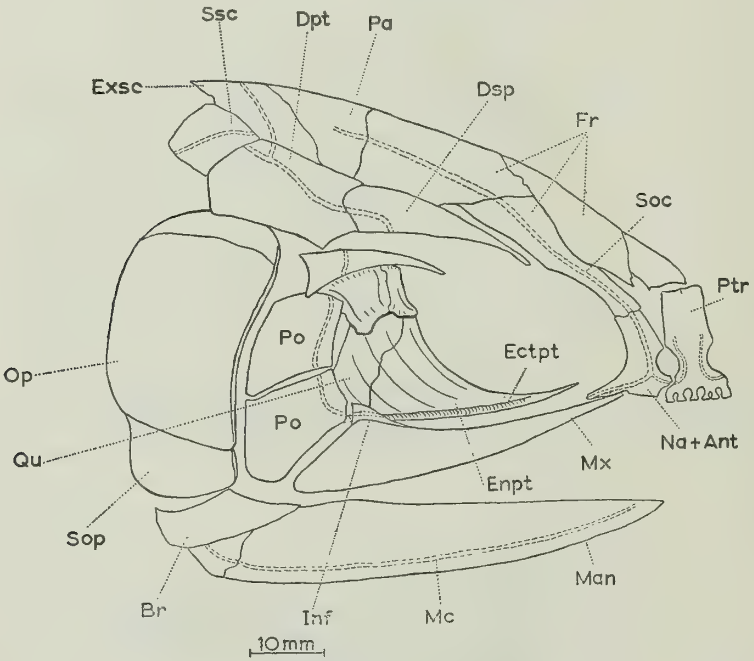


FIG. 16. *Ptycholepis bollensis* Agassiz. Sketch of a specimen from the Lias of Holzmaden, Germany, in the Tübingen Museum.

The dermosphenotic is broadened somewhat posteriorly, where it meets the dermopterotic, but narrows as it passes forwards. It borders the frontal laterally along most of its length, and forms part of the dorsal rim of the orbit. It does not, however, reach the nasal as in *Ptycholepis curta.*

The majority of the remaining description is based on a specimen (unnumbered) in the Tübingen Museum, from the Lias of Holzmaden, catalogued under the Keppler collection. The structure of the snout is typically Palaeoniscid, composed mainly of a prominent postrostral element. This bone passes from the frontal forwards and downwards and is then tucked back under to form part of the ventral surface. Posteriorly it is relatively narrow and its lateral edges parallel, but anteriorly it broadens considerably as it passes round the snout. Laterally it is indented to form the anterior rim of the nasal orifice. On either side of the postrostral there is a large nasalo-antorbital bone. The nasalo-antorbital does not vary much in width and borders the entire lateral edge of the postrostral. Ventrally it is prolonged back under the orbit and has a neat recess into which the posterior extremity of the maxilla fits. Posteriorly the nasalo-antorbital borders the orbit, and anteriorly the nasal orifice. Along its ventral edge it bears a row of small teeth, suggesting that this bone I have termed nasalo-antorbital represents not just a fusion of the nasal and antorbital bones, but also includes the premaxillary element (see specimen No. 4628 from Boll, again in the Tübingen Museum, which shows the articulations of the maxilla, nasalo-antorbital and postrostral perfectly).

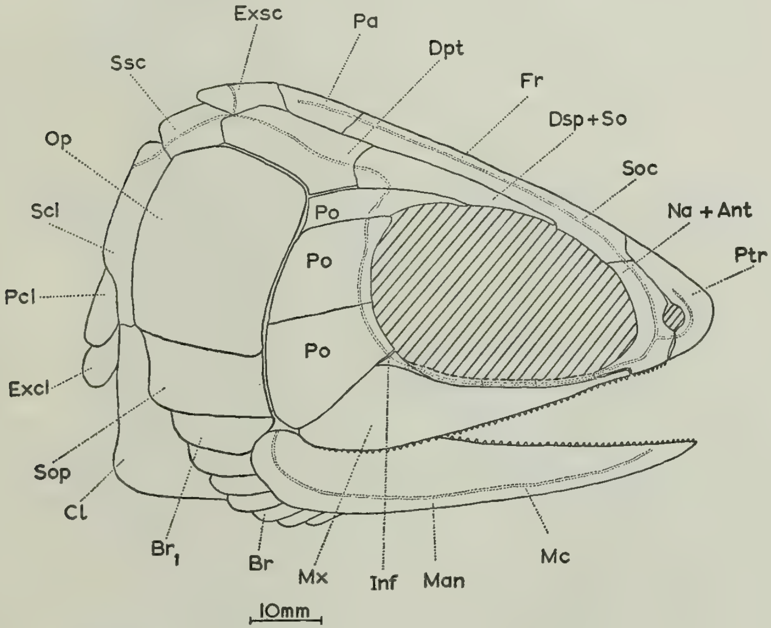


FIG. 17. *Ptycholepis bollensis* Agassiz. Restoration of skull and pectoral girdle.

The cheek region is characterized by the great development of the postorbital series of bones. This series completely covers the preopercular and excludes it altogether from the external surface of the skull. In the specimen of *Ptycholepis bollensis* from the Lias of Holzmaden, this series is completely preserved. There are three bones of which the first two are of roughly comparable size and shape, but the third, the most dorsal of the series, is much thinner and elongated. The first two border the orbit posteriorly, but the third forms part of the dorsal rim of the orbit, and fits neatly under the antero-ventral edge of the dermopterotic and the postero-ventral edge of the dermosphenotic. In shape it closely resembles the dermosphenotic but is much smaller. The edges of all three bones are distinct and there does not appear to be another series intervening between them and the orbit.

The maxilla and one infraorbital are well displayed on the same specimen. The maxilla extends from the first branchiostegal ray forward to where it meets the nasalo-antorbital. Posteriorly the maxilla is of triangular shape where it fits under the first postorbital, but as it passes forwards the maxilla tapers gently. The ventral border of the maxilla overlaps the mandible posteriorly, but in this region the border is not produced downwards so much as in earlier species.

The infraorbital is a small triangular bone firmly attached to both the upper border of the maxilla and to the antero-ventral corner of the first postorbital. The infraorbital sensory canal passes through this bone. The remaining bones of the infraorbital series, those which border the maxilla dorsally, are missing in the specimens examined. However, since the first one is present and the maxilla has a distinct ledge along its dorsal border, there is every reason to believe such a series was present.

The opercular bones together form a large quadrangular gill cover. The opercular is deeper than wide, approximately rectangular with a somewhat concave anterior border. The subopercular, although large, is much smaller than the opercular to which it is attached closely. It is much wider than deep and does not end in a sharp ventral angle as it does in *Ptycholepis curta.*

Immediately below the subopercular is the first branchiostegal ray. This ray is considerably enlarged and of distinctive shape, tapering to a point anteriorly. It appears to overlie the posterior extremity of the lower jaw. The remaining rays are smaller, about nine or ten in number, and the series ends with the median gular plate.

Lower jaw. The structure of the lower jaw could be well seen in a specimen of *Ptycholepis bollensis* from the Lias of Whitby (B.M.N.H. P 3691*a*) after mechanical preparation (Text-fig. 15). This specimen was figured by Woodward (1896, pl. 5, fig. 4), but the illustration shows nothing apart from the ornamentation. In the specimen the surangular bone forms the posterior dorsal corner of the mandible and has a deep recess for the articulation with the upper jaw. Below this articulatory facet the surangular is produced into a distinct ridge, and posteriorly behind the facet it forms a backward projection to the mandible. From this elbow-like projection the surangular runs down in a concave sweep to meet the angular. The angular is a much larger bone with little ornamentation dorsally, but with thick ridges of enamel running horizontally over its ventral region. Anteriorly the angular is thickened, making the junction with the dentary quite distinct. The remaining area of the admesial surface of the jaw is composed of the dentary. Ventrally the dentary has thickened ridges of enamel running more or less longitudinally, but nearer its superior border the ridges are turned upwards. The upper margin is not a straight line as in *Ptycholepis barboi*, but has a marked coronary prominence. The teeth are not shown in P 3691*a*, but on several specimens in the Tübingen Museum the dentition of the lower jaw is visible. There are two rows of small slightly rounded teeth running along most of the upper surface of the jaw.

Sensory canal system. The supraorbital canal commences well back in the parietal, and runs forward through the length of the frontal. Anteriorly it passes down into the nasalo-antorbital, where it joins the infraorbital canal.

The main cephalic division of the sensory canal crosses the antero-dorsal corner of the supracleithrum and passes forward through the dermopterotic. At its point of entry into the dermopterotic, it gives off the supratemporal commissure, which runs through the extrascapular. The main cephalic division then turns down through the posterior corner of the dermosphenotic as the infraorbital canal. The infraorbital canal passes round the anterior edge of the postorbitals, and down through the infraorbitals, finally entering the nasalo-antorbital. In the nasalo-antorbital it branches into two, the anterior branch passing into the postrostral where it ends blindly just above the nasal orifice. The posterior branch continues on through the nasalo-antorbital to fuse with the supraorbital canal. Most of the above account of the sensory canal system is based on specimen No. 8740 from Boll, in the Tübingen Museum.

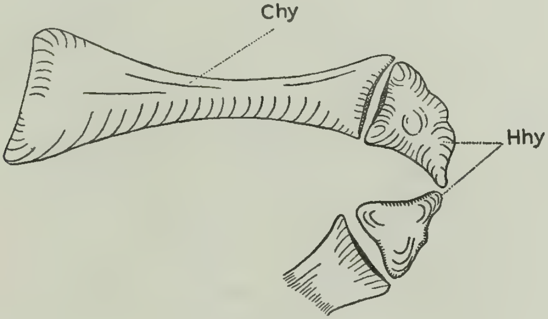


FIG. 18. *Ptycholepis bollensis* Agassiz. Ceratohyal and hypohyal. From a specimen from the Lias of Holzmaden, Germany, in the Tübingen Museum.

Palate. The palatoquadrate is very similar to that described by Stensiö (1921 : 211) for *Boreosomus arcticus*, and by Brough (1939 : 63) for *Ptycholepis barboi*. The palato-quadrate is a large ossification consisting of three principal elements, a quadrato-metapterygoid, an entopterygoid and an ectopterygoid (Text-fig. 16). In general shape the whole apparatus is triangular with its posterior margin almost vertical. The antero-dorsal margin is strongly concave and the ossification tapers almost to a point anteriorly. The most posterior bone is the quadrato-metapterygoid and is a large high bone. Dorsally it articulates with the orbitotemporal region of the neurocranium. The entopterygoid is also rather high and the distinct suture between it and the quadrato-metapterygoid is indicated in the sketch (Text-fig. 16). The entopterygoid forms most of the anterior portion of the palate. Beneath it is a narrow ectopterygoid running almost horizontally. This bone extends back to meet the quadrate. It is a much thickened ossification, and gives the edge of the palate a bevelled appearance. On the inner surface of the entopterygoid there is a distinct area bearing small tubercular teeth ; whether the quadrato-metapterygoid had a similar area could not be ascertained. The neurocranium must have been a stout ossification, because in one specimen in the Tübingen Museum (no number) the skull had been laterally crushed and the ossified neurocranium can be seen beneath the dermal bones. The most obvious portions are a distinct postorbital process and an ascending ramus of the parasphenoid.

Hyobranchial apparatus. Of the hyoid arch only the ceratohyal and the hypohyal can be seen (specimen No. 8739*c* in the Tübingen Museum). Both bones are stout with the ceratohyal cylindrical in cross-section (Text-fig. 18). The proximal ends of the ceratohyal are thickened, but the central region is a good deal thinner. The hypohyal is triangular in outline, well rounded and with a distinct facet for articulation with the ceratohyal.

Appendicular skeleton. The pectoral girdle is rarely seen and is invariably covered by the opercular bones. However, in yet another specimen in the Tübingen Museum, from Boll (no number), the pectoral girdle is well displayed (Text-fig. 17). The supracleithrum is a rather wide spatulate bone, but tapering to meet the cleithrum. Where the supracleithrum adjoins the cleithrum, there are two more bones of approximately the same size as one another, one is the postcleithrum and the other the extracleithrum. Both bones are oval in shape and there is very little ornamentation on them. The supracleithrum, postcleithrum, and extracleithrum all have a slight ridging on their posterior margins, but nothing to compare with the ornamentation of the other skull bones. The cleithrum is large and perfectly smooth, and this, together with the sparse ornamentation of the other girdle bone, suggest that the entire girdle was sunken and not exposed on the surface during life.

Nothing is seen of the other internal bones of the trunk because the squamation is thick and completely covers the skeleton. In specimen B.M.N.H. 19656 from Boll, the caudal region is reasonably clear, but there is no evidence of ossified vertebral rings and it appears safe to assume that the vertebral column was cartilaginous.

The pectoral fins contain stout fin rays which only articulate and divide distally. The more anterior rays are ornamented with fine longitudinal ridges of enamel, and show traces of small fulcra. The number of rays in the pectoral fin is between twenty-three and twenty-five.

The pelvic fins are smaller, and none of the lepidotrichia appears to be ornamented. There are from fifteen to twenty fin rays.

Unpaired fins. The dorsal fin arises well in front of the pelvics and has between eighteen and twenty-three fin rays.

Of the anal fin little trace can be found on any of the specimens examined in the B.M.N.H. The tail is hemiheterocercal and the scaly lobe short. The fin rays of the lower lobe are distantly articulated and finely divided distally.

Squamation. The body scales are highly ornamented and have been described at length in earlier works (see Aldinger, 1937 : text-figs. 85*b*, 87*b*). In the region of the pelvic fin three of the scales are modified ; these are ovoid in shape and considerably lengthened. They are narrowest posteriorly and twice the size of an ordinary scale. One or two of these modified scales also occur in front of the anal fin insertion. The course of the lateral line is marked by large clefts in the hinder ends of some of the scales it passes through, and its position is very low on the body wall. In particular, in one specimen in the Tübingen Museum, the course of the canal was marked by a pair of pores on each scale of the lateral line series, and occasionally an arcuate tubule.

Family SAURICHTHYIDAE

DIAGNOSIS. Elongate and slender fishes, with abbreviate-diphycercal tails. Dorsal fin far back, above the anal; the number of lepidotrichia in both exceeds that of the supporting radials. Radials of the dorsal fin either in one or two rows. Paired fins small. Radials of the pectoral fin only ossified in the Lower Triassic species, and the pelvic girdle is present as a distinct ossification only in the Triassic forms. Fulcra minute or absent. Long slender ribs present. Trunk wanting a continuous squamation, usually only four rows of scales, one dorsal, one ventral, and one lateral on either side supporting the lateral line, otherwise the body is naked (*Saurorhynchus brevirostris* (Woodward)). Maxilla of much the same shape as in the Palaeoniscoidea, firmly attached to the preopercular and the quadrato-jugal, and from within, to the ectopterygoid and dermopalatine. Hyomandibular is narrow and vertical, and without an opercular process. Quadrate and metapterygoid fused. The opercular apparatus consists of a single large opercular, but this bone possibly also incorporates a fused subopercular. Branchiostegal rays reduced, one on either side. Palate completely ossified, with paired vomers. The dentition consists of well-spaced, large conical teeth, with numerous intervening smaller teeth. Vomers and palate also bear teeth, but these are in the form of small rounded tubercles. Neurocranium completely ossified, with a large myodome, no basipterygoid process and no *processus craniospinalis*. There are two nasal orifices on either side and the supraorbital sensory canal passes between the two nasal openings. Head and opercular bones ornamented with striations and tuberculations. Notochord persistent, ossified vertebral elements are present in the Triassic forms, but absent in the Jurassic species.

REMARKS. This family contains two genera—the first *Saurichthys* Agassiz, into which all the Triassic forms are placed, and the second *Saurorhynchus* Reis, which contains only two species, both from the Lias.

Genus ***SAURORHYNCHUS*** Reis, 1892*b*

1844. *Belonostomus* Agassiz, **2**, pt. 2, p. 142, pl. 47*a*, figs. 3, 4 (in part).
1858. *Belonorhynchus* (?) Bronn, p. 12 (in part).
1925. *Acidorhynchus* Stensiö, p. 175.
1940. *Gymnosaurichthys* Berg, pp. 194, 408.

DIAGNOSIS. As for family (only genus).

TYPE SPECIES. *Saurorhynchus acutus* (Agassiz).

REMARKS. This genus was erected by Reis (1892*b* : 145) and incorporates the two Jurassic species, *S. acutus* (Agassiz) and *S. brevirostris* (Woodward). Berg (1940 : 194, 408) put the second species *brevirostris* into the new genus *Gymnosaurichthys* Berg, on account of its body being entirely naked. In almost every other respect *brevirostris* is very similar to *acutus* and I cannot agree with Berg (1940 : 194, 408) that the total absence of scales in the former is sufficient for the erection of a new genus *Gymnosaurichthys* for its reception.

The generic name *Saurorhynchus* was first used by Braun (1840 : 73) when he listed the species *Saurorhynchus tenuirostris*. When used by him it was a *nomen nudum*, but when Reis (1892*b* : 145) later used it to describe *Saurorhynchus acutus* the name became valid and as such must take preference over *Acidorhynchus* Stensiö (1925 : 175).

Saurorhynchus acutus (Agassiz)

(Text-figs. 19–22)

1844. *Belonostomus acutus* Agassiz, **2**, pt. 2, p. 142, pl. 47*a*, figs. 3, 4.
1844. *Belonostomus anningiae* Agassiz, **2**, pt. 2, p. 143 (name only).
1844. *Belonostomus tenellus* Agassiz, **2**, pt. 2, p. 143 (name only).
1858. *Belonorhynchus* (?) *acutus* (Agassiz) Bronn, p. 12.
1858. *Belonorhynchus* (?) *anningiae* (Agassiz) Bronn, p. 12.
1876. *Belonostomus acutus* Agassiz : Tate & Blake, p. 259.
1887. *Belonorhynchus acutus* (Agassiz) : Zittel, p. 222.
1888*a*. *Belonorhynchus anningiae* (Agassiz) : Woodward, p. 355.
1888*b*. *Belonorhynchus anningiae* (Agassiz) : Woodward, p. 147.
1890. *Belonorhynchus acutus* (Agassiz) : Woodward & Sherborn, p. 16.
1892*b*. *Saurorhynchus acutus* (Agassiz) Reis, p. 145 (in part).
1895*b*. *Belonorhynchus acutus* (Agassiz) : Woodward, p. 14, pl. 2, fig. 1.
1899. *Belonorhynchus acutus* (Agassiz) : Woodward, p. 456.
1921. *Belonorhynchus acutus* (Agassiz) : Hauff, p. 31.
1925. *Acidorhynchus acutus* (Agassiz) Stensiö, p. 175, fig. 58.
1938. *Acidorhynchus acutus* (Agassiz) : Hauff, p. 215.

DIAGNOSIS. A *Saurorhynchus* with a head between 10 and 15 cm. in length, and a maximum width of 10–15 mm. The height of the skull is usually from 20–30 mm., of which the mandible comprises approximately half. The head is from four and a half to five times as long as the maximum depth.

SYNTYPES. Fragmentary skulls (B.M.N.H. **P** 4268 and P 961*a*), both from the Upper Lias, Whitby.

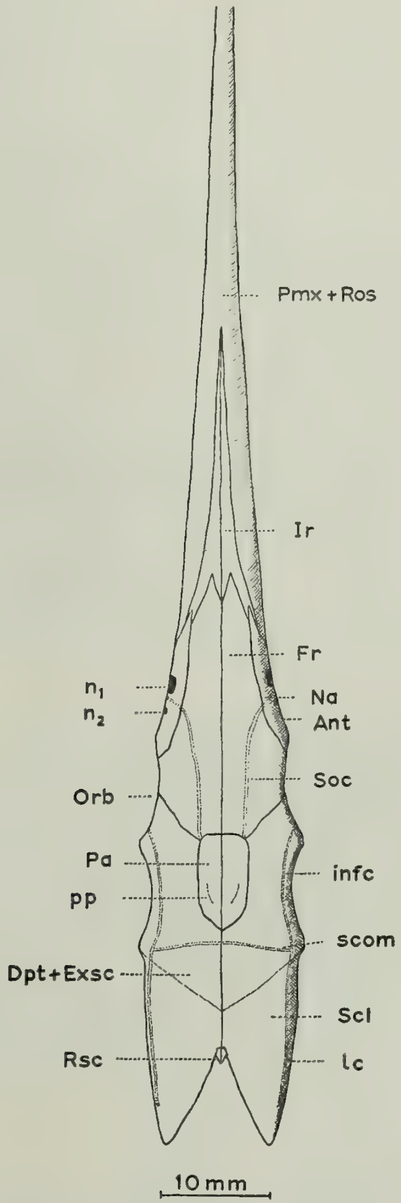
MATERIAL. Specimens in the B.M.N.H., the Sedgwick Museum Cambridge, the Oxford and Geological Survey Museums.

REMARKS. Although the types came from the Upper Lias of Yorkshire, all the remaining specimens in the B.M.N.H. are from the Lower Lias of Lyme Regis.

DESCRIPTION. *The skull.* The dermal roof is a completely fused shield, with individual bones very difficult to make out.

Stensiö (1925 : 89) found in the genus *Saurichthys* indications of a set of bones in front of the frontals, and more or less embedded in the roof of the rostralo-premaxillary. He was not sure of their true extent, but called the bones anterior postrostral elements which included the interrostrals. Two specimens of *Saurorhynchus acutus* (one in the Geological Survey Museum No. 492, the other from the Sedgwick Museum, Cambridge) show clearly the extent of these bones. There is quite definitely a pair which abuts not only on to the frontals as Stensiö (1925 : 89) supposes, but also on to the nasals (Text-fig. 19). I have called this pair of bones, which extends about three-eighths of the way along the rostrum, the interrostrals.

The paired frontals extend from in front of the nasals back almost to the posterior margin of the orbit. Stensiö (1925 : 89) thinks that on account of the considerable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n_1
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10 mm

Fig. 19. *Saurorhynchus acutus* (Agassiz). Skull roof, reconstructed, dorsal view.

extension forward on to the ethmoidal region, the frontals probably also include the homologue of the posterior postrostral elements of the Rhipidistids. Anteriorly the frontal bounds the nasal, antorbital and the interrostrals, but it does not come into contact with the rostralo-premaxillary as in *Saurichthys* (Stensiö, 1925 : 89). Posteriorly the frontals do not extend far enough round the orbit to meet the dermosphenotic (Text-fig. 20). The posterior edge of the frontals is fused to the parietals. In both *Saurorhynchus acutus* and *Saurorhynchus brevirostris* there is only one pair.

These parietals are small and form a comparatively tiny heart-shaped bone in the centre of the cranium, just to the rear of the orbits. Occurring on the surface of each parietal is a short line of pit organs similar to those of *Saurichthys*.

The rest of the cranial roof is composed of a sheet of bone of composite nature, containing the dermopterotic-extrascapular series. This sheet at its anterior end bounds the posterior edge of the orbits, the frontals and the parietals. It continues backwards beyond the opercular on either side. The lateral edge of the sheet is, after it leaves the orbit, distinctly concave, then further back it becomes convex (Text-fig. 19). The dermopterotic-extrascapular portion of the shield appears to have a suture line running back across it towards its posterior end, just behind the supratemporal commissure. This suture is indistinct, but runs backwards on either side meeting in the mid-line, midway between the parietals and the first ridge scute.

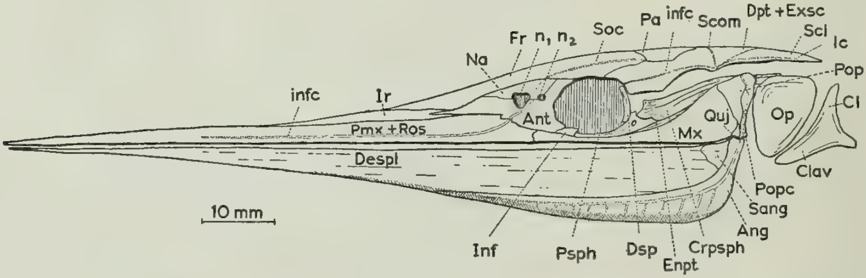

FIG. 20. *Saurorhynchus acutus* (Agassiz). Reconstruction of skull in lateral view.

The remaining portion of the shield extends backwards on either side to a point beyond the cranio-spinal process. It probably contains the suprascapular and the supracleithrum fused indistinguishably together. At its centre posteriorly it contains a small triangular bone, which is the most anterior dorsal ridge scute.

The ornamentation of enamel of all these bones including parietals, rostrals, frontals etc., is coarser than that found on the rest of the skull, and consists mainly of short stout striae. These run in a more or less longitudinal direction on the parietals, frontals and dermopterotic-extrascapular, whilst on the nasals they radiate downwards.

The orbit is large and while there is evidence in some specimens of a complete sclerotic ring, this appears not as a truly ossified bone but rather in the form of a calcified cartilage. The bones of the cheek and the infraorbital series do not often appear to be preserved, but by mechanical preparation of a few of the B.M.N.H. specimens some of the structures have been revealed.

In no specimen was a supraorbital bone located, but by analogy with other Saurichthyids and related forms, it must be assumed that either one or more supraorbital was present during life and that due to conditions of fossilization has since been lost. However, a small infraorbital bone occurs near the base of the orbit, abutting on the posterior ventral surface of the antorbital, and having every appearance of Stensiö's lachrymal (Text-fig. 20), while bounding the posterior margin of the orbit, a well-developed dermosphenotic can be seen. The dermosphenotic is a curved bone which does not fit neatly on to the skull roof, suggesting thereby the absence of another bone series—the supraorbital.

As with the supraorbital, the remaining infraorbitals are also missing. What Woodward (1895*b* : 16) describes as a suborbital is a narrow bone beneath the orbit, but in reality this is only the anterior portion of the parasphenoid. When fully prepared, in every case this narrow bar-like bone extended backwards, and always a large foramen became visible in it. This foramen is for the external carotid artery, which proves the bone to be the parasphenoid and not the suborbital.

The parasphenoid in the region of the floor of the orbit exhibits a strong convexity ventrally, but as it continues backwards it fuses with neurocranial elements, and is a ridged bar beneath the cranial shield and often extending beyond it.

It is true to say that the orbital series of bones was less well ossified than the surrounding dermal bones, and as a result is rarely preserved.

According to Woodward (1895*b* : 10, 16), the nasal opening is single on each side, and obliquely elongated. Stensiö (1925 : 90), however, has shown that in *Saurichthys* there are two nasal vacuities. On examination of *Saurorhynchus acutus* and *S. brevirostris* this also proved to be the case, the anterior nasal aperture being the larger of the two.

Stensiö (1925 : 90) called the bone containing these two apertures the nasalo-antorbital, because he recognized that it was formed as a result of the fusion of two bones (cf. Rhipidistid Crossopterygians). In one specimen of *Saurorhynchus acutus* in the B.M.N.H., the nasalo-orbital was clearly shown to consist of two bones, the nasal and the antorbital. Both bones were seen to enter into the formation of the apertures, the nasal forming the top half of the anterior nasal aperture and the antero-dorsal part of the posterior nasal aperture, the remaining portions of the apertures being bounded by the antorbitals (Text-fig. 20).

The maxilla is the same shape as that found in the Palaeoniscids, and is firmly fused on to the premaxilla. At its posterior end the maxilla unites with the preopercular, the suture line between them being almost obliterated. Both Stensiö (1925, fig. 21) and Woodward (1895*b* : 10) observed the maxilla, but Stensiö also recognized a preopercular. In neither *Saurorhynchus acutus* nor *S. brevirostris*, was it possible to establish with certainty whether or not a quadrato-jugal was present. The maxilla continues forwards and forms a thin bar beneath the orbit and fuses with the premaxilla just anterior to the orbital foramen. Interiorly the maxilla fuses with the ectopterygoid and dermopalatine. The quadrato-jugal is, however, present and is observable from the side as a very small triangular bone set between the posterior ventral corner of the maxilla and the anterior ventral corner of the preopercular. Together with the preopercular it enters into the jaw articulation.

The preopercular is smaller than the maxilla and is triangular in shape. It has a pronounced ridge running in a vertical direction near to its posterior edge. Behind this ridge the preopercular sensory canal travels upwards from the articulatory facet to the top of the preopercular. The posterior and anterior edges of the bone are slightly concave and approximately equal in height. Both the maxilla and the preopercular exhibit a strong rugosity similar to that found on the frontals and parietals.

Immediately behind the preopercular, although not actually in contact with it, is the opercular. The opercular is very much smaller than in the rest of the Saurichthyids. In shape it is deeper than broad, and there is no indication of its being succeeded by any branchiostegal rays. The ornamentation of the opercular consists of short striae which radiate outwards and downwards from the anterior dorsal corner.

The much elongated rostrum appears to be formed chiefly of one bone as in *Saurichthys* (Stensiö, 1925 : 89)—the rostralo-premaxilla. Running three-quarters of the length of this composite bone is a branch of the supraorbital sensory canal. The supraorbital canal presumably continues on up between the two nasal foramina as in *Saurichthys*.

Lower jaw. The lower jaw is just a little shorter than the upper, both being elongated forwards, and tapering strongly to their anterior extremities. The mandible is deepest posteriorly, its posterior border descending almost vertically from its articulation with the skull. This border is in most cases concave, whereas in *Saurichthys* it is normally convex.

The Meckelian cartilage is ossified and the outer surface is covered by three dermal bones, the angular, surangular and dentalo-splenial ; whilst on the inside is a long mixicoronoid (terminology from Stensiö, 1925). Since a double series of large teeth (B.M.N.H. P 965*b*) extends to the termination of the mandible, there can be no pre-symphysial bone.

The angular is the most posterior bone, and its hinder border descends in a slightly concave manner from the articulation with the upper jaw. This has the effect of making the deepest region of the mandible the most posterior. Along the length of the angular bone runs a branch of the sensory canal system (mandibular branch), but here it differs from that condition found in the other Saurichthyids in that it sends off ventrally numerous fine branches, which give the appearance of a series of vertical striations. This mandibular canal can be traced back through the jaw articulation and up into the preopercular. The angular participates directly in the mandibular articulation to the exclusion of the surangular. At its anterior end it tapers almost to a point, and its demarcation is clearly visible as it runs from the most dorsal posterior point in a strong concave sweep until it reaches this anterior extremity.

The surangular is a small bone which abuts the angular in the posterior dorsal region, and forms for a short distance the dorsal edge of the jaw. This bone is triangular in shape and fuses indistinguishably into the dentalo-splenial, which actually covers part of its anterior surface.

The dentalo-splenial forms the long tapering anterior portion of the mandible. Posteriorly it meets the angular along its ventral edge, whilst dorsally it abuts on to and over the surangular.

The ornamentation of the lower jaw generally consists of a superficial rugosity, not so well marked as that found on the dermal bones of the skull roof. The ornamentation on the angular bone runs in a vertical direction, while that on the dentalo-splenial is only found at the posterior end where it is horizontal.

Dentition. The dentition on the margin of both jaws is essentially similar. The teeth fall into two series and all are capped with enamel. Those comprising the larger series vary in height from 2–5 mm., those of the smaller series from 0·5–1 mm. The larger teeth are conical, pointed and curved backwards. Occurring in both the upper and lower jaws is a series of notches (Text-fig. 21) for the reception of the larger teeth of the opposite jaw. The notches and teeth alternate and allow the jaws to be tightly closed. The intermediate spaces between the larger teeth are filled with the small-tooth series. These are thin, sharply pointed and more numerous than the larger ones. The two sets occur along the whole length of the ventral surface of the rostralo-premaxillary and on to the anterior portion of the maxilla. On the lower jaw they occur along the dorsal edge of the dentalo-splenial almost up to the surangular.

The vomers and the anterior region of the parasphenoid are also provided with small teeth of a more rounded, almost stud-like variety. The mixicoronoid has teeth of even smaller size on some of its surface. In the large tooth-series the teeth get more robust posteriorly, and many show an absence of vertical striations basally of the enamel cap (Text-fig. 22). The dentition strongly suggests that the genus had a predaceous habit.

Neurocranium. An ossified neurocranium is present, both Woodward (1895*b* : 10) and Stensiö (1925 : 176) being in error in assuming that it was cartilaginous (Text-fig. 21).

The neurocranium forms one single ossification, there being no individual bones recognizable. The endocranium on the one specimen (G.S. 492) which I was able to prepare in acetic acid (Text-fig. 21), was unfortunately a little broken up in the optic region. However, several foramina could still be distinguished. I think the fenestra optica was much larger in this species than in the other Saurichthyids (Stensiö, 1925), the roof of it showing three foramina on either side.

The most anterior foramen was for the exit of nerve I, whilst that one immediately below and to the posterior of it was for the exit of a blood vessel. The foramen in this case has a groove running anteriorly from it with several small foramina within that groove. From its position this blood vessel must have been the *vena cerebralis anterior* (*vert.cart.ant.*). Above the canal for this vessel occurs another small foramen, and by analogy with other Saurichthyids (Stensiö, 1925) this must have been the exit for nerve IV.

The optic and other adjoining foramina are missing, but a distinct trigemino-facialis chamber occurs just anterior to the *processus ascendens* of the parasphenoid. On the same level as the trigemino-facialis chamber, but nearer to the edge of the neurocranium occur two more foramina, somewhat separated from the more posterior

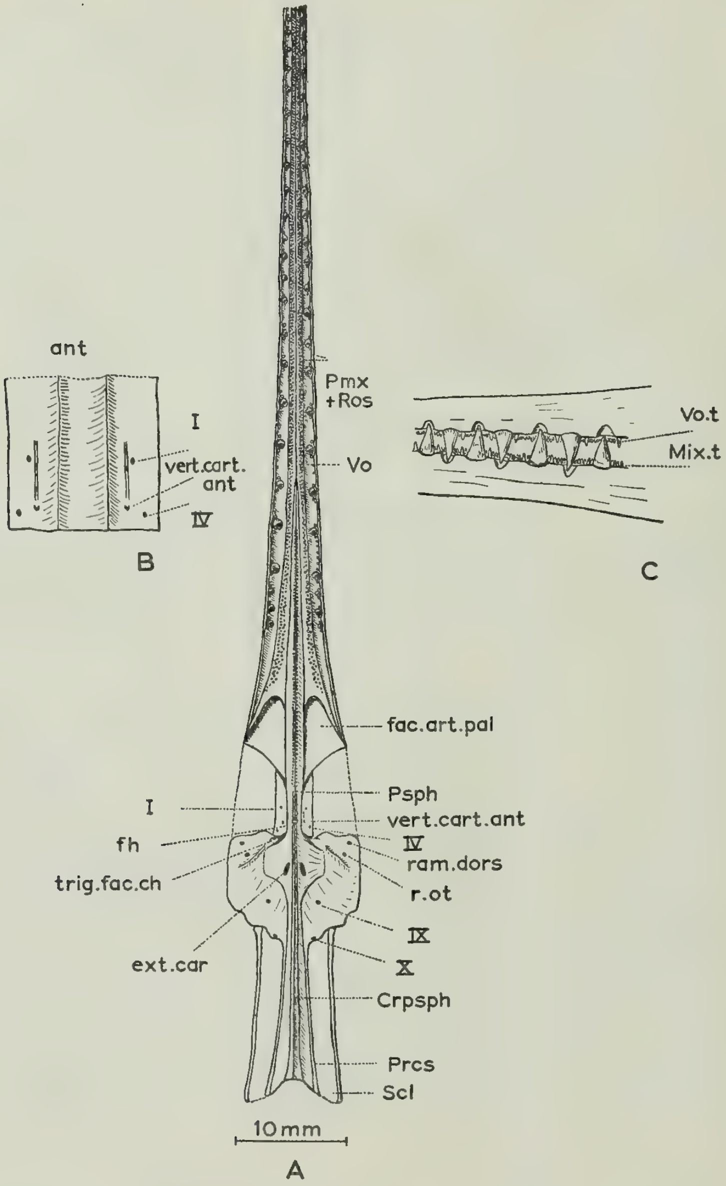
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FIG. 21. *Saurorhynchus acutus* (Agassiz). A, Neurocranium and palate, ventral aspect, from G.S. 492. B, Optic region of same specimen, ventral view, parasphenoid removed. C, Small portion of jaw of another specimen to show alternation of teeth and notches.

foramina by a distinct ridge. The more anterior of the pair transmitted branches of the *r. ophthalmicus superficialis trigemini* (*ram.dors.*), whilst the posterior member (*r.ot.*) transmitted the *ramus oticus*.

Only two further foramina were located, both well back on the neurocranium. The first was the exit for nerve IX and the more posterior for that of nerve X.

The occipital region is long and relatively narrow, being widest most posteriorly where it broadens somewhat to form the cranial spinal processes. It is covered very nearly completely throughout its length by the parasphenoid.

Of the other bones of the skull little is observable. The hyomandibular (Sedgwick Museum J 36707) is long and in an oblique position, somewhat broadened antero-dorsally, its axis being much inclined forwards, occupying a similar position to that found in the Palaeoniscids. Covering the dorsal end of the hyomandibular is a small ossification here called the dermohyal. This bone is more posterior in position than the bone Px of Stensiö (1925 : 92), fitting between the dorso-anterior end of the maxilla and the dermopterotic-extrascapular. Ossified elements such as the autopalatine, entopterygoid, ectopterygoid and dermopalatine are also present. The entopterygoid only is visible on most of the specimens. From within the ectopterygoid and dermopalatine are firmly united with the maxillae.

Palate. In the palate the paired vomer is a long narrow bone traversing the whole length of the underside of the rostrum (G.S. 492). At its posterior end it is separated into its two constituent bones by the intervention of the parasphenoid (Text-fig. 21). The parasphenoid stretches about one-third of the distance up the vomers and where it ends the two vomers are divided by a suture for the remaining two-thirds of their length. Consequently the vomer is widest posteriorly, the two ends diverging to border the articulatory surface for the reception of the autopalatine.

The parasphenoid itself extends posteriorly from the vomers right back over the occipital region of the neurocranium. The anterior portion of this bone is dagger-shaped, and as it continues back over the orbital region it narrows somewhat. In this area it is pierced by the *fossa hypophyseus*. Immediately behind the fossa the parasphenoid fans out into the *processus ascendens*, which covers a large portion of the labyrinth region of the underlying neurocranium. The true extent of the *processus ascendens* is difficult to ascertain since the bone is very much broken in this area. However, the canal on either side for the external carotid artery is clearly discernible. Posteriorly to the *processus ascendens* the parasphenoid again narrows and exhibits a distinct crest, but as it continues on back over the occipital region the bone expands and becomes much wider posteriorly, whilst the crista becomes less pronounced and finally tapers out. The parasphenoid extends so far back in this species that it covers a portion of the lower side of the most anterior vertebra.

Sensory canals. The supraorbital sensory canal has its origin posteriorly at a point where the frontals fuse with the parietals. It then runs forward on either side and passes down between the two nasal vacuities to fuse with the infraorbital canal. From below the antorbital the supraorbital canal runs about three-quarters of the length of the rostralo-premaxillary. The other portion of the infraorbital canal forms a direct continuation of the cephalic portion of the lateral line. Thus the two together form a canal on either side of the posterior head shield, which runs from the orbit back to the posterior end of the shield (Text-figs. 19, 20). Its forward continuation down through the dermosphenotic cannot be traced, mainly because of the bad state of preservation of the latter. The two cephalic portions of the lateral line of each side are joined by the supratemporal commissure. This passes across the dermopterotic-extrascapular. Finally, the course of the mandibular which is a direct continuation of the preopercular canal has already been described.

The similarity between this system and that found in the Palaeoniscids has already been pointed out by Stensiö (1925 : 213).

Appendicular skeleton. No remains of the skeleton of the unpaired fins have been found, although some traces of the paired fins can be seen. Immediately behind the opercular in several specimens occurs a triangular-shaped bone with its edges facing ventrally, caudally and antero-dorsally. This bone is the fused cleithrum and clavicle and served for the articulation of the pectoral fin.

Axial skeleton. The notochord was persistent, and the neural and haemal arches much expanded, both bearing spines. In the caudal region the short slender neural spines become elongated to be symmetrical with the haemals. In no specimen is there satisfactory indication of intramuscular bones.

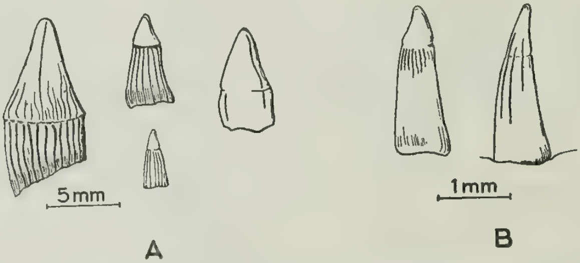

FIG. 22. A, Teeth of *Saurichthys* sp. B, Teeth of *Saurorhynchus acutus* (Agassiz) to show variation in striation.

Squamation. The body appears to have been covered with only four rows of bony scutes, one dorsal, one ventral and one lateral on either side (supporting the lateral line).

Systematic position. The genus *Saurorhynchus* (*Acidorhynchus*) according to Stensiö (1925 : 175) differs from *Saurichthys* in the following respects :

> " 1. Smaller lengthening of the rostrum.
> 2. No or very slight ganoine ornamentation.
> 3. Certain differences in the shape and relations of the dermal bones.
> 4. Rather much reduced opercular.
> 5. Absence of vertical striations on the teeth basally of the enamel cap."

I have examined the above points and find that only two of the five are valid differences. Taking them in order, first the " smaller lengthening of the rostrum ": measurements were made on all the skulls of *Saurichthys* and *Saurorhynchus* that were available, and a direct comparison made in each case of the length of the rostrum against the length of the rest of the head. Plotting these measurements graphically, both genera fall on the same straight line (Text-fig. 80), and there is no significant difference in the relative length of the rostrum between the two.

The second difference, " no or very slight ganoine [enamel] ornamentation " is also incorrect, since all the skull roofs of *Saurorhynchus* that I have examined show an ornamentation, in some cases quite thick, of tubercles and striae of enamel. The third and fourth differences, " certain differences in the shape and relations of the dermal bones " and a " rather much reduced operculum " are perfectly valid. By comparing the above description with those given by Stensiö (1925) and Lehman (1952) for the earlier genus *Saurichthys*, these differences will be apparent. The reduced opercular is particularly noticeable. Finally, the " absence of vertical striations on the teeth basally of the enamel cap " in the genus *Saurorhynchus* is incorrect. Several teeth of *Saurorhynchus* I have examined show striations basally of the enamel cap (Text-fig. 22), whilst others of *Saurichthys* show an absence of such striations (Text-fig. 22).

Although three of Stensiö's (1925 : 175) five reasons for founding the genus *Acidorhynchus* are no longer valid, the two remaining, plus such features as a less heavily ossified neurocranium in *Saurorhynchus* and the absence of intramuscular bones and ossified pelvic girdle, and the peculiar pectoral girdle, make the retention of the genus necessary to incorporate the Liassic species *acutus* and *brevirostris*.

" HOLOSTEI "

Family Furidae

Diagnosis. See Woodward, 1895*b* : 285. (Eugnathidae).

Genus ***OSTEORACHIS*** Egerton, 1868

Diagnosis. Trunk elongate, paired fins large, but pectorals considerably larger than pelvics. Dorsal fin opposite the pelvic fins, the anal fin immediately behind the pelvics. Dorsal and anal fins triangular and the caudal fin deeply forked. Fulcra present on all the fins, distal articulations of the lepidotrichia very close. Opercular much larger than the subopercular. Dentition : marginal teeth large, well spaced and slightly curved. Teeth on the splenial and ectopterygoid smaller, long and slender. Distinct pleuro- and hypocentra. External skull bones ornamented with tubercles and striae of enamel. Scales thin possessing distinct peg-and-socket articulations.

Type species. *Osteorachis macrocephalus* Egerton.

Remarks. Three species only of this genus have been described, *Osteorachis macrocephalus* Egerton and *Osteorachis granulata* Egerton both from the Lower Lias of Lyme Regis, and *Osteorachis leedsi* Woodward, from the Oxford Clay of Peterborough.

Osteorachis macrocephalus Egerton

(Text-figs. 23–27)

1839. *Pachycormus ? macrurus* Agassiz, **2**, pt. 2, p. 113, pl. 58*a*, fig. 3.
1868. *Osteorachis macrocephalus* Egerton, p. 500.
1872. *Osteorachis macrocephalus* Egerton : Egerton, no. 5, pl. 5.
1876. *Harpactira (Harpactes) velox* Egerton, pp. 441, 576.
1885. *Heterolepidotus grandis* Davis, p. 293, pl. 7.
1890. *Harpactira velox* Egerton : Woodward & Sherborn, p. 92.
1890. *Osteorachis macrocephalus* Egerton : Woodward & Sherborn, p. 136.
1890. *Platysiagum grandis* (Davis) Woodward & Sherborn, p. 151.
1895*a*. *Osteorachis macrocephalus* Egerton : Woodward, p. 204, pl. 7, fig. 10.
1895*b*. *Osteorachis macrocephalus* Egerton : Woodward, p. 325.
1897. *Osteorachis macrocephalus* Egerton : Woodward, p. 385.

DIAGNOSIS. An *Osteorachis* of large size reaching up to a metre in length. The length of the head is about a quarter of the total length of the fish. The body is fusiform, approximately seven times as long as deep. Opercular considerably deeper than broad, much larger than the subopercular. The latter is at least three times as broad as deep. Scales finely and closely tuberculated. Neurocranium heavily ossified.

SYNTYPES. B.M.N.H. P 3654, P 3655, P 3649 and P 3648*a*, from the Lower Lias, Lyme Regis.

MATERIAL. Specimens in the B.M.N.H. and the University Museum, Oxford.

REMARKS. Agassiz (1839 : 113, pl. 58*a*) described an imperfect tail from the Lower Lias, Lyme Regis as *Pachycormus ? macrurus*. This specimen is now in the Oxford Museum (No. J 3050). I have examined the specimen but find that its relationship to the genus *Osteorachis* is not certain. If in fact it can be proved subsequently to be the tail of an *Osteorachis*, then the species *Osteorachis macrocephalus* Egerton is no longer valid, and the name *Osteorachis macrurus* (Agassiz) would take preference, with this specimen as holotype.

DESCRIPTION. *The skull.* The skull roofing bones are well preserved in B.M.N.H. P 875. This is a small specimen, probably of a young individual on which the suture lines are still clearly marked. On the large skull of B.M.N.H. P 3648*a* only the demarcation between the frontals is at all clearly shown.

The frontals are by far the largest of the bones forming the skull roof (Text-fig. 23). They are much the same width along their entire length, although they narrow somewhat anteriorly. The median suture line is well shown, being characteristically wavy, with one large acute lobation posteriorly. Behind the frontals are the much smaller parietals. These are remarkably asymmetrical, and, like the other skull bones, are covered with a coarse tuberculation. Posteriorly the frontals are in contact with the dermosphenotics which, although smaller than the other skull roofing bones, are large in comparison with those found in *Caturus* and other allied genera. The remaining roofing bones making up the posterior portion of the skull are the dermopterotics. These are much longer than the parietals and form a distinct edge to the roof in that region. They abut on the parietals, frontals and dermosphenotics on their inner margins. The remaining bones represented in B.M.N.H. P 875 are those seen posterior to the parietals, and are the extrascapulars, not displaced otic bones, as Woodward (1895*b* : 328) erroneously described them. The roofing bones of the snout are more difficult to interpret, no one specimen showing them *in situ*. However in a specimen in the Oxford Museum (Ox. M. J 3033), a small somewhat displaced bone near the anterior end is probably a nasal (Text-fig. 24). By comparison with *Caturus* it is reasonable to suppose that a pair of nasals did in fact occur anteriorly to the frontals.

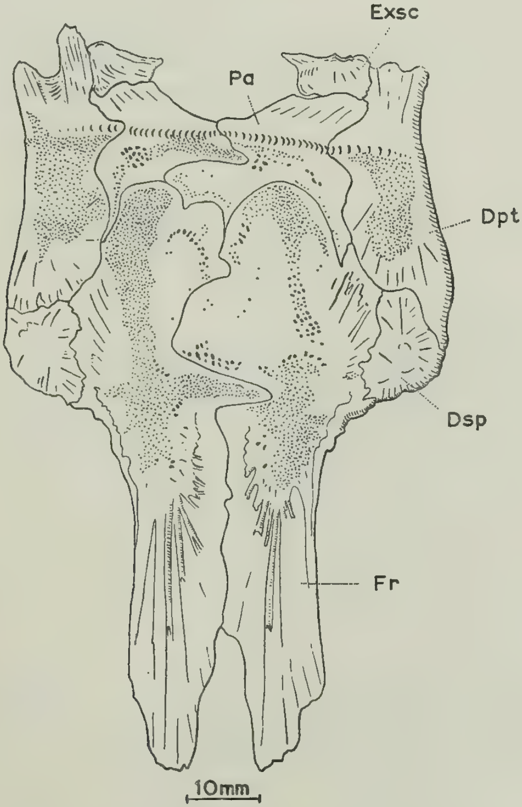

FIG. 23. *Osteorachis macrocephalus* Egerton. Dorsal view of skull roofing bones. From B.M.N.H. P 875.

Specimen Ox. M. J 3033 is more or less laterally compressed, and much fractured and crushed, although the left orbital surface has remained practically intact. From this specimen much of the cheek bone arrangement can be derived. However, the region represented is that anterior to the opercular apparatus, and specimens B.M.N.H. P 876*x* and P 3648 must be examined to show the latter.

The premaxilla is a small bone bearing from eight to ten closely set teeth, of much the same appearance as those found on the maxilla. A fragment of bone appearing above the premaxilla is undoubtedly the remains of a rostral bone. The maxilla is a long slender bone, thickened anteriorly and deepened behind. The tooth arrangement on this bone is of interest since one of the generically distinguishing features between this species and *Furo* is the enlargement of the inner clustered teeth. In specimen Ox. M. J 3033 Woodward (1895*a* : 205) maintained that the maxilla and mandible bore only a single series of teeth, and that the cluster of teeth appearing below the maxilla pertained to the ectopterygoid, whilst those above the dentary to the splenial. By acid development I have been able to show that this is incorrect, as on both the upper and lower jaws there are often two to three rows of teeth.

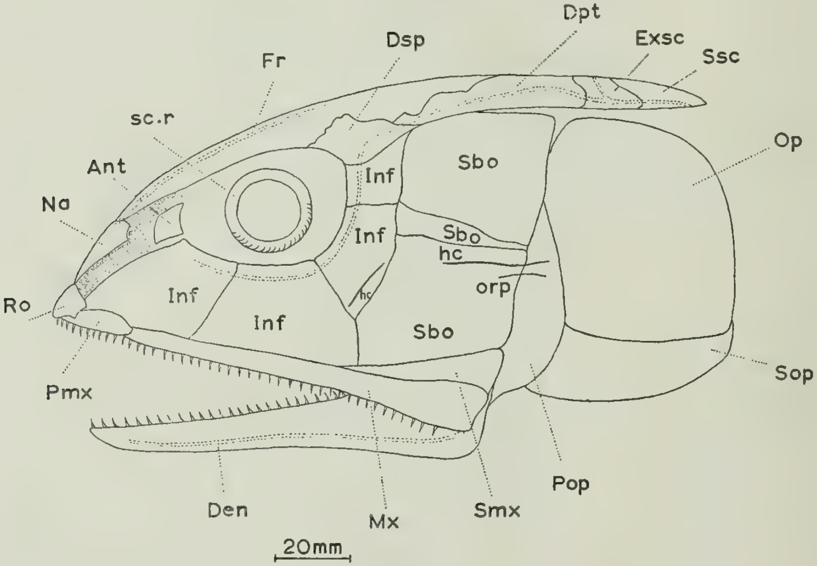

FIG. 24. *Osteorachis macrocephalus* Egerton. Reconstruction of the dermal bones of the skull in lateral view.

The outer teeth are long, slender, hollow and pointed, the inner ones being similar in shape, but smaller. These inner teeth are not very much different from those covering the ectopterygoid and splenial. The fact that most of the palatal bones are covered by teeth makes the total absence of teeth on the parasphenoid difficult to understand. Above the posterior margin of the maxilla a single supramaxilla occurs. This is a small bone, distinctly pointed at its anterior end.

Immediately in front of the preopercular two fair sized bones can be seen, one above the other, with a smaller one separating them. These represent the suborbital series. They are very similar in proportion to those found in *Caturus*, the similarity in the respective cheek bones of these two genera being striking.

The opercular itself is a large bone rounded above and deeper than wide. It is covered externally with a fine and close tuberculation, with areas of large tubercles interspersed. The subopercular beneath is more drawn out, being much wider than deep (cf. P 3648). The preopercular separating these two bones from the orbital series is a longer, thinner, much curved bone, similar to that found in the genus *Caturus*.

The orbit has a completely ossified sclerotic ring, around which fragments of further ossification are to be seen. These fragments represent the intraorbital series so characteristic of the Holostei. This series consists of five plates. The two posterior ones are small, and form together the hinder edge of the orbit. The two ventral plates are much larger, approximating in size to those of the suborbital series. They form the lower margin of the orbit and extend down on to the maxilla. The last plate only remains as a fragment, but obviously completed the margin of the orbit anteriorly. This fragment is termed a prefrontal by Woodward (1895*a* : 205) but is more probably an antorbital.

Lower jaw. The lower jaw is intact in Ox. M. J 3033 except for its posterior extremity. It shows a high coronoid process and the general shape of the jaw can be followed. The quadrate is represented in B.M.N.H. P 3654 and is relatively large with a well-developed articulatory process for the lower jaw. The hyomandibular is seen in B.M.N.H. P 3654 and has a long opercular process. This process is somewhat unusual in that it has a thin sheet of bone connecting both its upper and lower extremities with the hyomandibular proper. Returning to Ox. M. J 3033, between the rami of the mandibles a complete gular plate is observable, two-thirds as long as broad with a normal series of branchiostegal rays behind it.

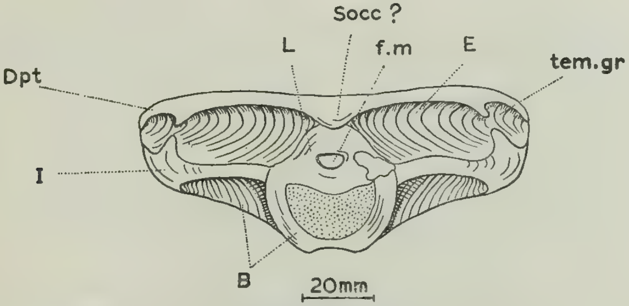

FIG. 25. *Osteorachis macrocephalus* Egerton. Hind view of neurocranium. From B.M.N.H. P 3648*a*.

Neurocranium. Beneath the dermal roof is a remarkably well-ossified neurocranium, much heavier and stouter than in any other species of Holostean fishes I have examined. The following account is based on one specimen (B.M.N.H. P 3648*a*), the few other specimens of the species known being all completely flattened and thus unsuitable for acid development.

The general shape of the neurocranium differs considerably from that of the other Holostei. It is almost twice as broad as deep, thereby giving the whole neurocranium a much flattened appearance. The ossification is complete, as in *Dapedium*, there being no remnants of cartilaginous areas. Consequently suture lines are almost obliterated and careful study is needed to interpret the demarcation of the various bones.

This task is the most difficult in the postorbital region. A backwardly and downwardly directed projection above the foramen magnum I interpret as a supraoccipital (Text-fig. 25), but since no suture lines are visible I do so with reservation. From its position the bone around the foramen magnum is presumably the lateral occipital, which together with the epiotics, make up the rest of the neurocranium in this region. Abutting on the epiotics and lateral occipitals is a large and well-defined intercalar. This forms the base of the temporal groove, which in this species is long and well developed, giving a large surface area for the insertion of the trunk muscle ligaments. The provision of such broad and large grooves reflects the size of the muscles necessary to compensate the very heavy skull.

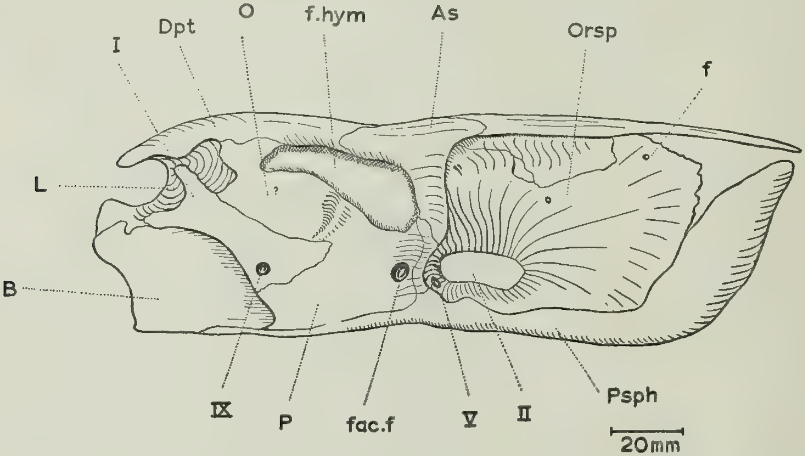

FIG. 26. *Osteorachis macrocephalus* Egerton. Neurocranium in lateral view. From B.M.N.H. P 3648*a*.

The basioccipital is a stout bone bordering the notochordal pit, and contributes to the formation of the lateral wall of the neurocranium. The intercalar too forms part of the lateral wall and the suture lines between it and the surrounding bones are well shown (Text-fig. 26). From the ventral region of the intercalar arises the ninth nerve. Dorsally this bone extends back into an irregular projection, similar to that described by Rayner (1948 : 292) in *Caturus*, for the attachment of ligaments from the suprascapular. The remainder of the lateral wall in the postorbital region is made up of the prootic and opisthotic. The opisthotic is quite large and bears the posterior half of the hyomandibular facet, besides forming the wall of the otic capsule. The prootic covers a larger area than the opisthotic and posteriorly is indented to take the anterior half of the hyomandibular facet. The most anterior portion of the facet is borne by the autosphenotic. Only one recognizable foramen is found in the prootic, the so-called facial foramen. This foramen transmitted the hyomandibular branch of the facial nerve.

The orbital surface is relatively easy to interpret (Text-fig. 27). The autosphenotic forms a large portion of the dorso-lateral region. The extent of the other orbital bones, pterosphenoid, prootic, basisphenoid and orbitosphenoid, can all be seen from Text-fig. 27. The optic foramen is large and confluent with the infra-orbital fenestra. There is a complete bony interorbital septum, with several foramina near its anterior end. The myodome is large, its two orbital openings being separated by the narrow stem of the basisphenoid. The cavity of the myodome extends back for about 2 cm. and is walled by the prootic and basisphenoid, whilst the floor is formed by the parasphenoid. Near its anterior end the roof bears an entrance for the hypophysis.

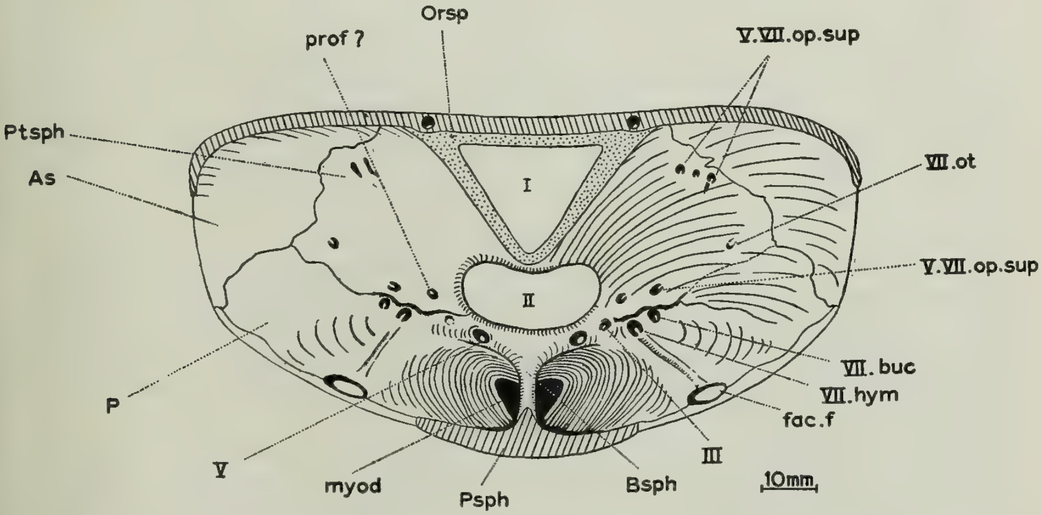

FIG. 27. *Osteorachis macrocephalus* Egerton. Neurocranium as if cut vertically just anterior to the optic foramen, showing the orbital surface. From B.M.N.H. P 3648*a*.

There is no true facial chamber as in *Caturus*. The main branch of the trigeminal has a fairly large foramen, in a similar position to that seen in *Caturus* (Rayner, 1948, fig. 7). Slightly dorsal to V is a smaller foramen, which transmitted the oculomotor nerve. From this last foramen a distinct ridge runs for some distance towards the lateral edge of the orbital surface. This ridge probably represents the demarcation between the pterosphenoid above and the prootic beneath. Under this ridge occur two more foramina, the larger one serving in life to transmit the hyomandibular branch of the VIIth, which passes down through the facial foramen. A well-marked canal can be seen running between the exit of the hyomandibular and the facial foramen. Beyond the foramen for the hyomandibular lies the other smaller foramen and this transmitted the buccal branch of the VIIth. The pterosphenoid bears several foramina. Of these, the one nearest the optic foramen possibly served for the exit of the profundus. Continuing outwards, the next upwardly directed foramen served for the passage of the superficial opthalmic. Towards the roof of the orbit and still in the pterosphenoid are several smaller foramina. These downwardly directed foramina were for the secondary branches of the superficial ophthalmic, supplying sensory organs (neuromasts). The remaining foramen in the pterosphenoid is that furthest from the mid-line, and was probably for the exit of the otic branch of the facial nerve.

The parasphenoid is a much broadened bone in this species (Text-fig. 26). It extends posteriorly on to the basioccipital which forms the floor of the neurocranium in that region. Passing forwards, the parasphenoid still maintains its broadened form and curves sharply upwards to meet the skull roofing bones. The absence of teeth of any type on the parasphenoid seems peculiar since this form has every appearance of a carnivorous feeder.

Sensory canal system. The course of the supraorbital canal can be traced on the frontals of B.M.N.H. P 875. It runs along the middle of each bone, and gives off a series of smaller radiating canals which pass out from it over the anterior surface of the frontal. The supraorbital canal continues on down into the nasals. The infraorbital canal can only be traced for a short distance through the anterior edges of the two posterior infraorbitals (Text-fig. 24), but the mandibular canal can be traced the length of the dentary.

Both the postmaxillary and supramaxillary sensory lines can be seen on Ox. M. J 3033. The supramaxillary line starts on the preopercular and runs forward across the dorsal region of the third suborbital. The anterior division of this sensory line runs more obliquely downwards through the surface of the postero-ventral corner of the second infraorbital. The postmaxillary line commences just below the supramaxillary line, in the preopercular and it only runs for a short distance into the posterior dorsal region of the third suborbital.

Appendicular and axial skeleton. As with most of the Holostei, the vertebrae are not completely ossified, there being distinct hypo- and pleurocentra. The fins are identical in general character with those of *Furo*, and there is little to be added to previous descriptions. The pectoral girdle is not shown on any of the specimens I have examined, but on B.M.N.H. P 3655 the pelvic girdle is well displayed. It consists of two bones, one somewhat displaced. These bones are not large, and are expanded posteriorly, but I can see no resemblance to an " hour-glass " shape attributed to them by Woodward (1895*b* : 327).

Squamation. The scales exhibit peg-and-socket articulation, and the ornamentation is rather characteristic. Often they are covered in tubercles which on some of the abdominal scales pass into conspicuous striae on the posterior halves.

Genus ***HETEROLEPIDOTUS*** Egerton, 1872

1861. *Brachyichthys* Winkler, p. 47.
1868. *Eulepidotus* Egerton, p. 505.

DIAGNOSIS. Holostean fishes of moderate size, hardly distinguishable from *Furo*. They differ from *Furo* in having a more deeply fusiform body and smaller teeth on the dentary and maxilla. Further, the vertebral elements are more heavily ossified in *Furo* than in all but the smallest species of *Heterolepidotus*. The squamation also differs in the two genera, *Furo* having pectinated scales, while those of *Heterolepidotus* are serrated but not normally pectinated.

TYPE SPECIES. *Heterolepidotus rhombifer* (Agassiz).

Heterolepidotus rhombifer (Agassiz)

(Text-figs. 28–30)

1836. *Semionotus rhombifer* Agassiz, **2**, pt. 1, p. 228, pl. 26*a*.
1837. *Lepidotus fimbriatus* Agassiz, **2**, pt. 1, p. 247, pl. 33*b*.
1849. *Lepidotus fimbriatus* Agassiz : Williamson, p. 444.
1849. *Semionotus rhombifer* Agassiz : Williamson, p. 444, pl. 41, fig. 9.
1868. *Eulepidotus fimbriatus* (Agassiz) Egerton, p. 505.
1872. *Heterolepidotus latus* Egerton, no. 2, pl. 2.
1887. *Heterolepidotus fimbriatus* (Agassiz) Zittel, p. 204.
1890. *Eugnathus latus* (Egerton) Woodward & Sherborn, p. 78.
1895*b*. *Heterolepidotus latus* Egerton : Woodward, p. 304.
1924. *Heterolepidotus* ex. aff. *latus* Egerton : Rüger, p. 731, text-figs. 6, 7.
1939. *Heterolepidotus latus* Egerton : Brough, p. 76, figs. 34–39.

DIAGNOSIS. A *Heterolepidotus* of large size, attaining a length of 70 cm. Length of the head about a quarter of the total length of the fish, but shorter than the maximum depth of the trunk. The external skull bones are not extensively ornamented. The orbit is small and the scales serrated posteriorly. The total length of the fish is only three and a half times the greatest depth of the body. The dorsal fin is opposite to the pelvic fins with its posterior border immediately opposite the anterior border of the anal fin, which it much exceeds in size. The lepidotrichia are stout and numerous, and except in the caudal fin have no articulation over the proximal half of their length. They bifurcate distally and are formed of many small segments. Fulcra are small, but present on all the fins. Tail is hemiheterocercal, not deeply forked.

HOLOTYPE. *Heterolepidotus rhombifer* (Agassiz) a young individual of the species, B.M.N.H. P 3620 from the Lower Lias, Lyme Regis. The original type of *Semionotus rhombifer* Agassiz (1836).

MATERIAL. Specimens in the B.M.N.H. and Geological Survey Museum.

REMARKS. In his synonymy of *Heterolepidotus latus* Woodward (1895*b* : 304) includes *Dapedium fimbriatum* described by Agassiz (1834 : Feuill. 9 and 35 : **2**, pt. 1, p. 196). The specimen of *D. fimbriatum* came from Häring in the Tyrol, and is probably Triassic in age, and most certainly not Liassic since there are no outcrops of the latter in that area. The original which was in the Munich Museum was destroyed in the war, and consequently was not accessible to the present author. However, from the description and plate given by Agassiz, together with the locality (i.e. not Liassic), it is obvious that *Dapedium fimbriatum* is not synonymous with *Heterolepidotus latus* Egerton and must be removed as a separate species. Further "*Heterolepidotus*" *fimbriatus* (Agassiz) is not synonymous with the other Triassic species from that area, *Heterolepidotus striatus* (Agassiz).

In 1836 Agassiz described and figured *Semionotus rhombifer* from the Lower Lias of Lyme Regis and since this is synonymous with *Heterolepidotus latus* Egerton, but was described far earlier, then it must take priority over Egerton's species. The specific name is thus *Heterolepidotus rhombifer* (Agassiz).

Description. *Neurocranium.* No complete description of the structure of the neurocranium of this genus has so far been produced. The following description is drawn chiefly from specimen No. 60123 in the Geological Survey Museum, which consists of a dorso-ventrally flattened neurocranium, with the parasphenoid and vomers complete. The specimen comes from the Lower Lias of Lyme Regis.

Although it is considerably crushed, almost all the individual bone sutures and nerve foramina could be detected after treatment of the surface with formic acid. Posteriorly the basioccipital forms the notochordal pit, but no sutures can be seen in that region to indicate the demarcation between the lateral occipitals and the basioccipitals. As in *Caturus* (Rayner, 1948, fig. 3) there is no supraoccipital, the epiotics protruding from under the parietals to form a dorsally rounded region to the back of the neurocranium (Text-fig. 28). To either side of the epiotics lie the dermopterotics. These form the roof of an extensive temporal groove, in which the anterior extremities of the trunk muscles had their insertion during life. A similar temporal groove is found in the Teleosts. Beneath the epiotics are the lateral occipitals. These form a large portion of the hind wall, and at the same time border the foramen magnum. The intercalars are beautifully preserved and in hind view form a lower boundary to the temporal groove.

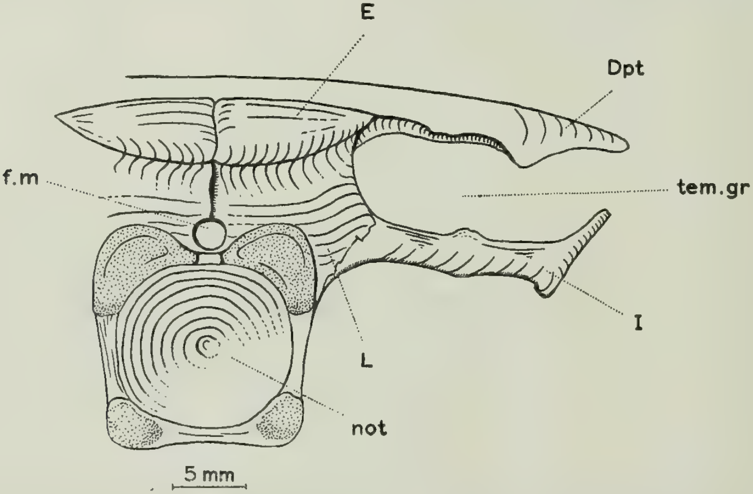

Fig. 28. *Heterolepidotus rhombifer* (Agassiz). Reconstruction of the neurocranium in hind view.

The lateral wall of the skull although completely flattened dorso-ventrally is still sufficiently undisturbed as to leave all the constituent bones in their relevant positions (Text-fig. 29). The intercalar is the most distinctive ossification and forms a large extent of the lateral wall. It is roughly triradiate in appearance, and is clearly distinguished by radiating fibres which stretch forward and downwards as in *Caturus*. Between the two more anteriorly directed processes of the intercalar is a distinct notch through which the vagal nerve was transmitted. The intercalar forms the upper, posterior and anterior margins of the vagal foramen, whilst the lower border is made up by an extension of the basioccipital. Anterior to the vagal foramen and a little above it, but still within the intercalar, the glossopharyngeal nerve had its exit. Anterior again to the intercalar is a somewhat fragmented prootic. Because of this fragmentation the origin of the seventh nerve and the

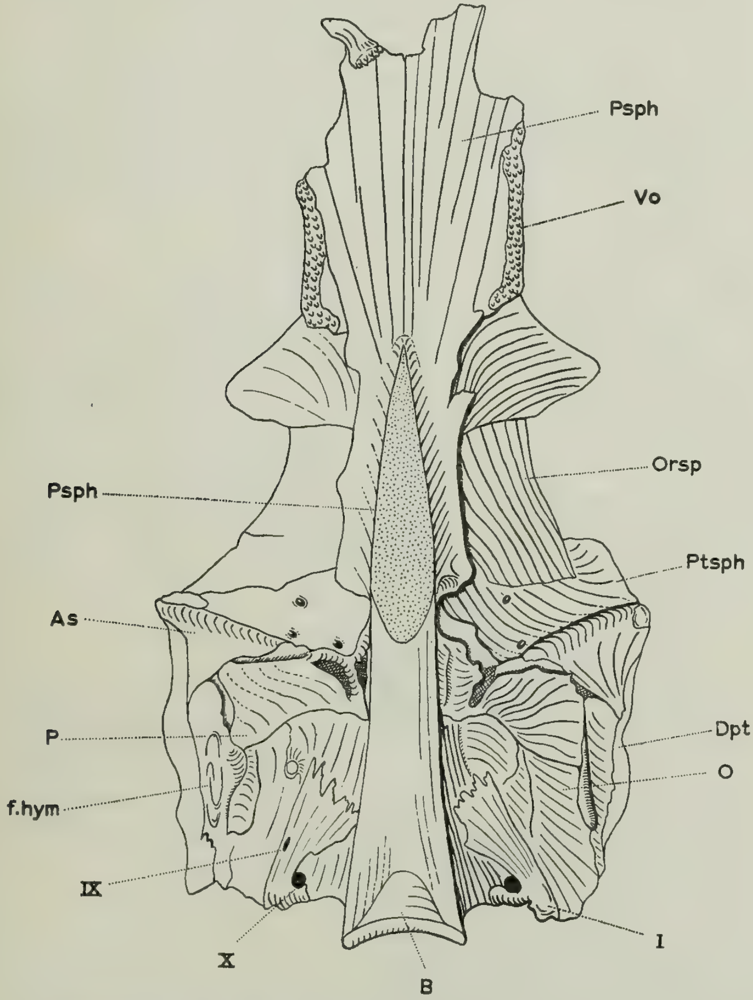

FIG. 29. *Heterolepidotus rhombifer* (Agassiz). Neurocranium in ventral view, slightly diagrammatic. From G.S. 60123.

subsequent passages of its component branches can be clearly traced (Text-fig. 30). The root of the seventh nerve goes back down through the prootic via a large foramen, posterior in position to the orbital surface. The hyomandibular branch of the seventh passes backwards and outwards on to the surface of the prootic, its passage being marked by a distinct groove. The buccal branch passes forwards and upwards and out on to the orbital surface via a small facial foramen. Through this facial foramen the jugular vein must also have been transmitted. The palatine branch of the seventh had a different course, passing forwards and downwards under a small bridge of prootic bone and out into the floor of the myodome. Ventral to the origin of the seventh nerve and running well beneath the surface of the prootic is a pronounced channel along which one of the branches of the internal carotid artery probably passed.

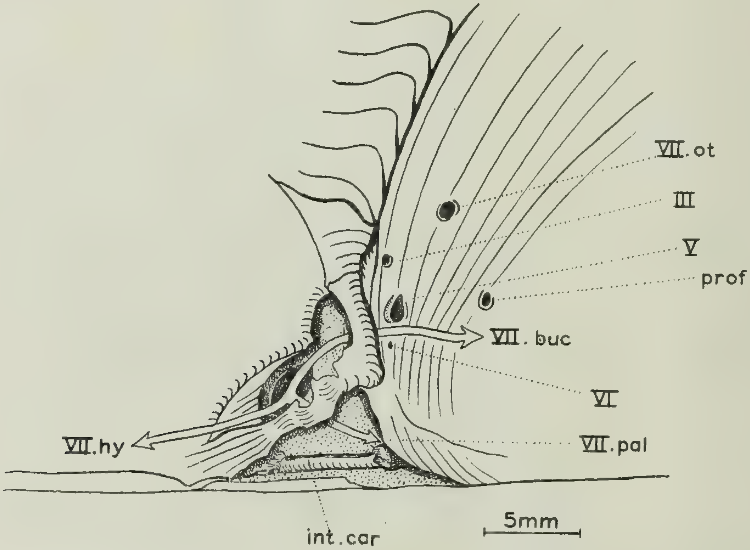

Fig. 30. *Heterolepidotus rhombifer* (Agassiz). Lateral view of neurocranium to show exits of the facial nerve. From G.S. 60123.

In the posterior otic region there appears to be another ossification. This bone fills in that region of the lateral wall from the prootic back to the intercalar. In my opinion it is obviously a quite separate ossification from that of the prootic and the intercalar, and must be termed an opisthotic. This conclusion is reached after examining all the three bones, which show lines of growth only compatible with three individual centres of ossification. The importance of the opisthotic in the Furidae will be dealt with in this discussion. Dorsally the opisthotic bears the hyomandibular facet, but the facet terminates anteriorly before it meets the autosphenotic. The autosphenotic is a large stout bone with a pronounced post-orbital process.

The orbital surface has been pushed forwards in fossilization, and ventrally has suffered from crushing. As a result it is difficult to deduce the size and depth of the myodome, but it was probably small as in *Caturus*.

The bony intraorbital septum appears complete, with the pterosphenoid and orbitosphenoid regions completely smooth. Immediately in front of the facial foramen is a large oval foramen which transmitted the trigeminal nerve. Ventrally to this is a much smaller foramen which probably served for the exit of the seventh cranial nerve. Dorsally to it are two more foramina, the first, the smaller of the two transmitted the third cranial nerve, whilst the second transmitted the otic branch of the facial nerve. Passing inwards towards the optic foramen is one more recognizable foramen which in life might have served for the passage of the profundus.

The parasphenoid is an elongated bone with a posterior smooth portion behind the orbits, and with a longer toothed portion in front. The teeth are small, granular and rounded, and form a dense series on the bone surface. Posteriorly this toothed area finishes in a gentle curve, but anteriorly in a distinct point. The bone continues forwards in front of this toothed region to form a smooth shelf beneath the vomers. Posteriorly it is bifurcated where it abuts the basioccipital. There is an appearance of a pair of small basipterygoid processes (Brough, 1939 : 81), but I can see no trace of an ascending process.

The structure of the vomers in this specimen appears different from that described by Brough (1939 : 81) from specimen B.M.N.H. P 7564, there being a narrow elongated area of vomer on either side of the parasphenoid bearing somewhat larger teeth than those found on the parasphenoid.

For a full description of the remainder of the fish see Brough (1939 : 76).

Genus ***CATURUS*** Agassiz, 1834

1833. *Uraeus* Agassiz, **2**, pt. 1, p. 12 (*non* Wagler, 1830).
1844. *Conodus* Agassiz, **2**, pt. 2, p. 105 (name only).
1851. *Strobilodus* Wagner, p. 75.
1858. *Endactis* Egerton, no. 4.
1866*a*. *Thlattodus* Owen, p. 55.
1866*b*. *Ditaxiodus* Owen, p. 107, pls. 4, 5.

DIAGNOSIS. Trunk long and fusiform. Pectoral fins large, exceeding the pelvics in size. Dorsal fin in advance of the anal, both triangular. The dorsal fin arises opposite or immediately behind the pelvics. Caudal fin hemiheterocercal and deeply forked. External skull bones and opercular apparatus only feebly ornamented with small tubercles and striae of enamel. Dentition : teeth on both the upper and lower jaws large and arranged in a sparse series. Teeth on the palatine and splenial smaller, those on the other palatal bones minute and granular. Maxilla long and straight sometimes slightly arched. Opercular deep, broader below than above. Subopercular smaller but of moderate size. Squamation : scales deeply overlapping and as broad as deep, feebly ornamented in part by tubercles and weakly crimped. Snout somewhat pointed and the cheek plates thin.

TYPE SPECIES. *Caturus furcatus* Agassiz.

Caturus chirotes (Agassiz)

(Text-figs. 31–36)

1836. *Eugnathus chirotes* Egerton, p. 368 (name only).
1842. *Eugnathus chirotes* Agassiz, **2**, pt. 2, p. 102, pl. 57*b*.
1844. *Conodus ferox* Agassiz, **2**, pt. 2, p. 105 (name only).
1890. *Eugnathus* (?) *chirotes* Agassiz : Woodward & Sherborn, p. 77.
1895*b*. *Caturus* (*Conodus*) *chirotes* (Agassiz) Woodward, p. 344, pl. 7, figs. 2, 3.

DIAGNOSIS. See Woodward, 1895*b* : 344.

HOLOTYPE. Imperfect fish, B.M.N.H. P 3643 from the Lower Lias, Lyme Regis.

MATERIAL. Specimens in the Geological Survey Museum Nos. 489 and 60124, both from the Lower Lias, Lyme Regis.

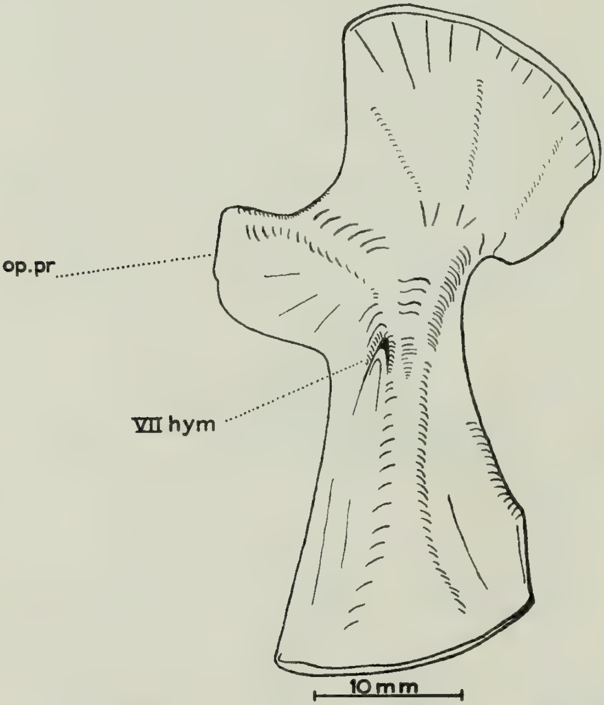

FIG. 31. *Caturus chirotes* (Agassiz). Right hyomandibular, external view. From G.S. 489*a*.

DESCRIPTION. The genus has been adequately described by Woodward (1895*b* : 344) and Rayner (1941, 1948 : 288). The following is in the form of a series of notes to supplement these accounts.

Hyoid arch. The hyomandibular is a stoutish bone in a nearly vertical position (G.S. 489*a*). It has a thickened, distinctly rounded head which articulates with the neurocranium by a deep articulatory facet in the prootic. The opercular process is well developed and lies at right angles to the main axis of the bone. A thickened strengthening ridge runs down from the opercular process to the base of the hyomandibular (Text-fig. 31). The foramen for the hyomandibular nerve is near the centre of the bone, just dorsal to the junction of the lower edge of the opercular process. The distal end of the hyomandibular is not quite so rounded as its head, but it is again strengthened for articulation with the symplectic and epihyal.

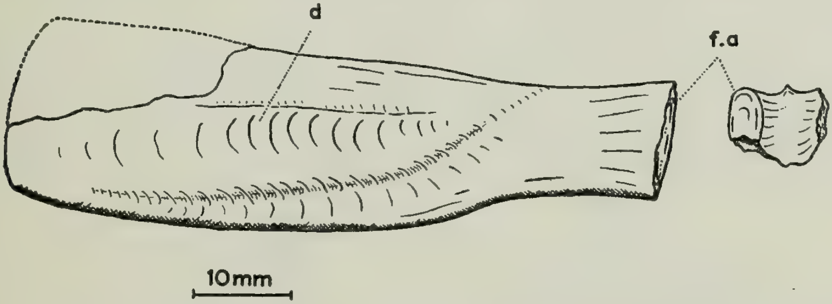

FIG. 32. *Caturus chirotes* (Agassiz). Ceratohyal and hypohyal of the left side. From G.S. 60124*b*.

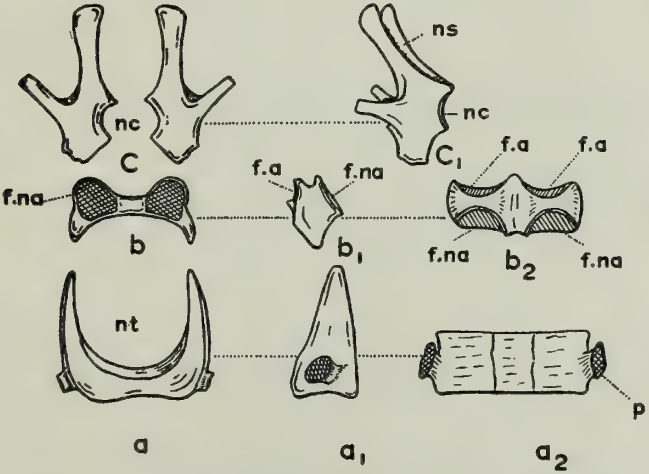

FIG. 33. *Caturus chirotes* (Agassiz). Caudal vertebra ; *a*, a_1, a_2 hypocentrum ; *b*, b_1, b_2 pleurocentrum ; *c*, c_1, neural arch. From G.S. 60124*c*.

A fragment of the epihyal remains between the hyomandibular and the ceratohyal in G.S. 60124, and this suggests that the epihyal was of comparatively small size.

In contrast the ceratohyal is a stout ossification, much thickened ventrally (Text-fig. 32). A distinct groove runs along it, first forwards and then upwards, disappearing before reaching the anterior end of the bone. Here the bone is considerably thickened, with a well-marked articular surface for the hypohyal.

Of the hypohyal only the dorsal half remains in G.S. 60124*b*. However, from the size of its articulatory facet it must have been a stout bone.

Vertebrae. The vertebrae of *Caturus* show a very primitive condition (Zittel, 1887 : 228). In this species each segment of the whole body shows two ossifications, an anterior pleurocentrum and a posterior hypocentrum, which together embrace the notochordal space. The pleurocentra bear articular facets for the neural arches which are wedged between them. In the caudal region the neural arches are divided into distinct halves, there being not only a cleft neural spine as in *Caturus furcatus*, but a complete division through the arch. The hypocentra have pronounced parapophyses in the trunk region for the articulation of the ribs. In the tail they bear haemal arches.

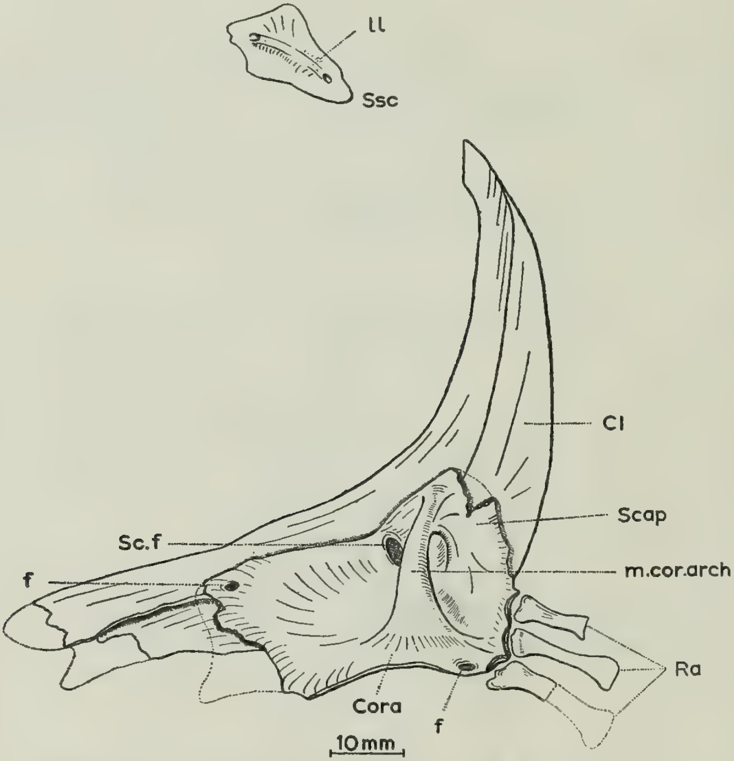

FIG. 34. *Caturus chirotes* (Agassiz). Internal view of right cleithrum and pectoral girdle. From G.S. 60124*d*.

Pectoral girdle. This has been extracted almost in its entirety from G.S. 60124*d* (Text-fig. 34). The suprascapular is a small bone which articulates with the skull in the region of the epiotics. Passing through the suprascapular is a branch of the sensory canal system which joins anteriorly with that from the extrascapular. Although the supracleithrum and postcleithrum are lost in this specimen, I have examined them on other specimens. The supracleithrum is considerably elongated and broadens somewhat ventrally. From its most ventral extremity it bears a narrow prolongation, which fits under the cleithrum. The sensory canal passes obliquely across it out on to the body scales. The postcleithrum is smaller than the supracleithrum and elliptical in general shape.

The cleithrum is a much curved bone with its anterior edge considerably thickened. The primary portion of the pectoral girdle is not cartilaginous as in the modern Holosteans *Amia* and *Lepidosteus*, but is completely ossified. The scapulo-coracoid is roughly rectangular in outline, the longer edge abutting against the cleithrum ; posteriorly it projects beyond the cleithrum and bears the glenoid surface, with which the three radials of the pectoral fin articulate (a similar condition is described by Rayner (1937 : 66) in *Leptolepis coryphaenoides*). Dorsally the scapular region has in it a large scapular foramen. On its inner surface the scapulo-coracoid bears a stout mesocoracoid arch, posterior to this foramen. The mesocoracoid arch is much more delicate in *Leptolepis coryphaenoides* (Rayner, 1937 : 66). In the lower Teleosts generally, it is very narrow while in the higher Teleosts it is absent (Boulenger, 1904*a* : 167). The ventral base of the mesocoracoid arch is pierced by the posterior diazonal nerve. There is no foramen for the anterior diazonal nerve and this must have passed in front of the mesocoracoid arch. One other small foramen is present, well forward in the coracoid region.

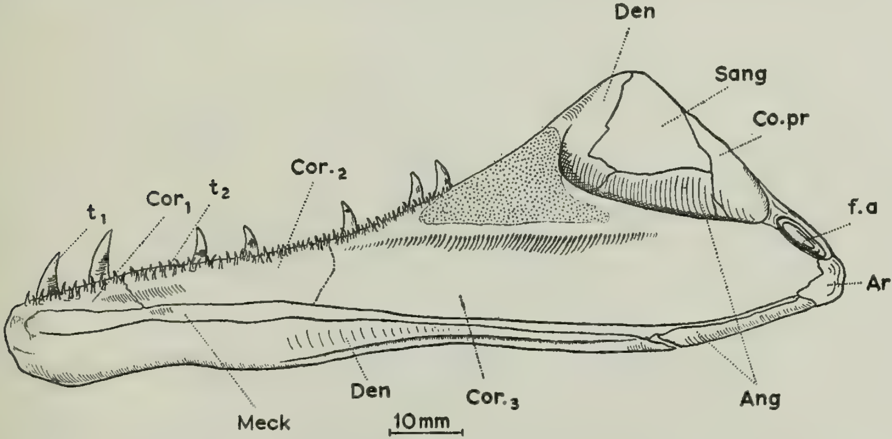

FIG. 35. *Caturus chirotes* (Agassiz). Inner view of right lower jaw. From G.S. 60124*e*.

The fin itself consists of twenty to twenty-five dermal rays inserted into a very short scaly lobe.

Lower jaw. Rayner (1948 : 291) has already partially described the lower jaw of *Caturus porteri* from an isolated mandible B.M.N.H. P 967. This description can usefully be supplemented by a further account of a complete lower jaw which

I have removed from a specimen of *Caturus chirotes* (G.S. 60124*e*).

The jaw consists of a dentary, angular, surangular, articular, coronoids and an ossified mento-Meckelian and shows a close resemblance to that of *Amia calva* (Text-fig. 35).

The dentary bears between ten and twenty large curved teeth, the anterior of which curves backwards, whilst the more posterior ones point forwards. There are at least two coronoids and probably three. If in fact there are these three separate coronoids, then the resemblance to *Amia* is striking. These bones make up most of the inner surfaces of the jaw, and dorsally bear numerous teeth. Dorsally on the most posterior coronoid (III) is a roughly triangular area covered in minute teeth.

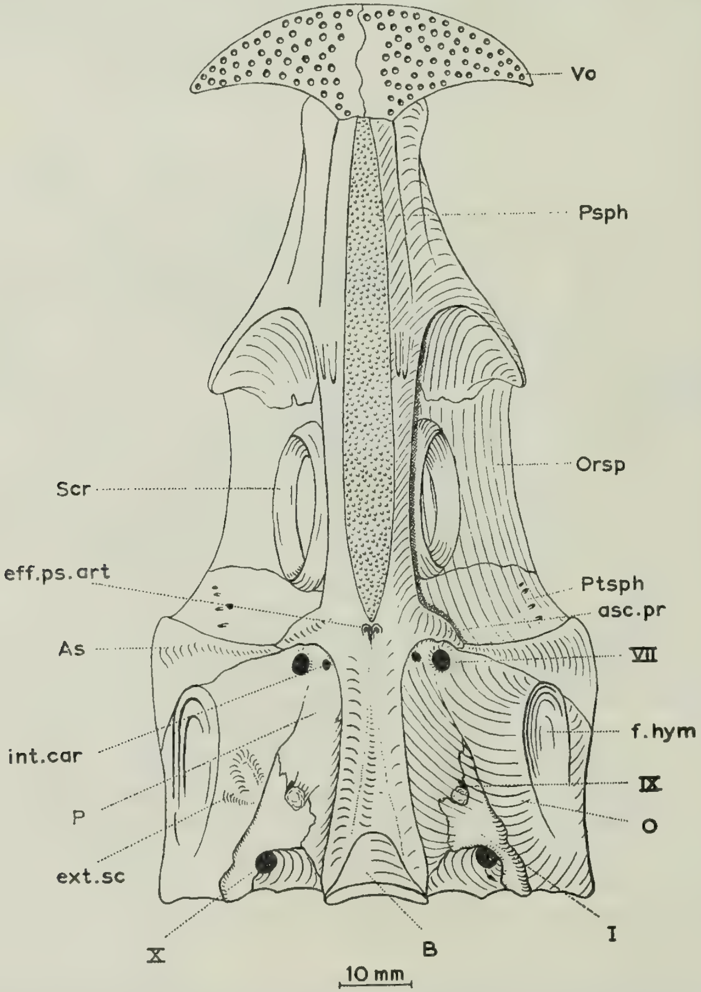

FIG. 36. *Caturus chirotes* (Agassiz). Neurocranium in ventral view. Right side somewhat restored. From G.S. 60124*f*.

From this point these bones bear teeth along their dorsal margins. These slender, sharply-pointed teeth are smaller than those borne by the dentary and far more numerous. The Meckelian bone is completely ossified, in contrast to the condition found in *Amia* and *Lepidosteus*. Posteriorly it forms the articular region which bears the articular fossa for the quadrate. Continuing upwards it forms an ossified coronoid process, which borders the angular and part of the surangular. The angular forms a large portion of the posterior quarter of the jaw. Above it are the triangular surangulars. All the suture lines in this region are well marked and easily discerned.

A large gular plate is found between the mandibles.

Skull and neurocranium. At first sight there seems little to add to what Woodward (1897 : 293) and Rayner (1948 : 289) have already said on the skull of *Caturus*. However, neither of these authors mentions a sclerotic ring in this genus, although in *Caturus chirotes*, two perfectly preserved sclerotic rings have appeared during acid treatment of G.S. 60124*f*. Text-fig. 36 shows a ventral view of the neurocranium, and from it several structures omitted by Rayner (1948) can be seen.

The parasphenoid is an elongate bone, with its anterior two-thirds covered by small sharp teeth. These are confined to an area near the centre of the bone as can be seen from Text-fig. 36. The ascending process passes backwards and upwards to meet the autosphenotic. In the mid-line in the region of the ascending process are two small foramina. These served for the passage of the efferent pseudobranchial arteries up into the parasphenoid. The transverse commissure between these two vessels, which exists in some Teleosts and which is recorded by Watson (1925 : 837) in the " Kansas Palaeoniscid " from the Coal Measures, could have existed since they are so close together, but there is no direct evidence of this. Anteriorly, the parasphenoid meets the paired vomers. Each vomer is much curved, almost sickle-shaped, and covered with long slender teeth. This contrasts with a statement by Woodward (1895*b* : 330) in which he maintains that the vomers in the genus *Caturus* bear teeth only at their anterior edges. The parasphenoid near its posterior extremity bifurcates to accommodate the basioccipital. Running down the centre of the parasphenoid posteriorly is a well-marked groove, which widens and deepens as it passes backwards. Finally, in the lateral wall of the neurocranium, above the intercalar and between it and the lateral occipital, is a further ossification. This is quite distinct and is clearly an opisthotic.

Family SEMIONOTIDAE

DIAGNOSIS. See Woodward, 1895*b* : 49.

Genus ***DAPEDIUM*** Leach, 1822

1833. *Tetragonolepis* Agassiz, **2**, pt. 1, pp. 6, 181 (in part).
1836. *Amblyurus* Agassiz, **2**, pt. 1, p. 220.
1845*b*. *Aechmodus* Egerton, p. 367.
1873. *Omalopleurus* Costa, p. 59, pl. 5, fig. 2*a*, *b*, *c*.

DIAGNOSIS. See Woodward, 1895*b* : 128.

TYPE SPECIES. *Dapedium politum* Leach.

Remarks. Most of the members of the genus *Dapedium* come from the English Lower Lias (particularly Lyme Regis). A few come from the Lower Lias of Alsace-Lorraine, and the remainder from the Upper Lias of Germany and France.

Dapedium sp.

(Text-figs. 37–41)

Material. A small isolated neurocranium from the Lower Lias of Stonebarrow, Charmouth. *Prodactylioceras davoei* zone, Green Ammonite Beds (Lower Limestone, Bed 123a). The specimen is in the B.M.N.H., registered Number P 11189.

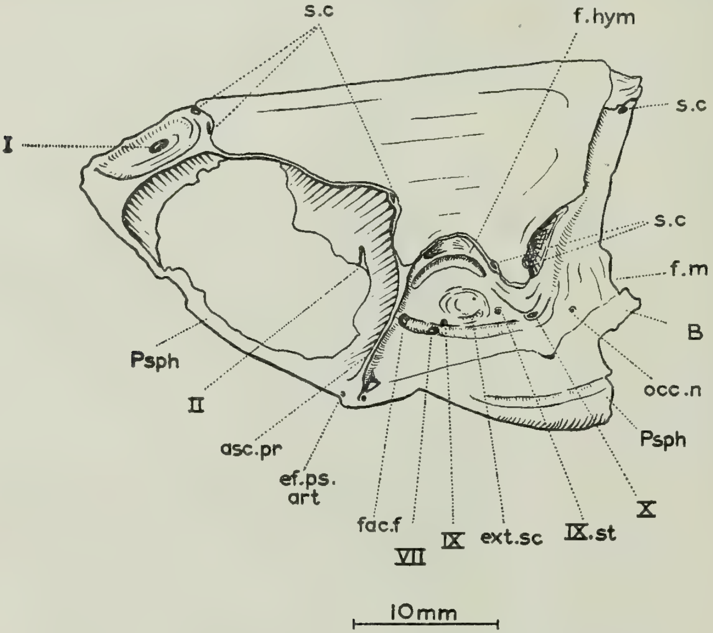

Fig. 37. *Dapedium* sp. Neurocranium in lateral view. From B.M.N.H. P 11189.

Description. *Neurocranium.* Only four specimens containing neurocrania are known of this genus. All of them have been previously described. The earliest description was published by Woodward (1893 : 563) consisting of a brief note on specimen B.M.N.H. P 3541. A few years later Frost (1913 : 219) gave a more extended description of specimen B.M.N.H. P 11177, and finally in 1948 Rayner published her paper on Holostean neurocrania, based on the other two specimens. One of these came from the Bath Museum (M.1280) and the other from the British Museum (Natural History) No. P 11189.

A re-examination of these four specimens showed that the two described by Woodward and Frost were so poorly preserved as to be useless for the determination of formina and suture lines. The third British Museum specimen (B.M.N.H. P 11189) seemed suitable for acid development. This was done and gave a complete neurocranium free from all surrounding matrix. Since both sides of the specimen are now visible, confirmation of existing foramina can be obtained by comparing one side with the other.

The skull of *Dapedium* is much more solidly constructed than that of its close relative *Lepidotes*, the ossification being complete (Text-fig. 37). The neurocranium is roofed by a continuous plate of membrane bone which has been formed by the fusion of the parietals, frontal and dermopterotic. This plate almost covers the entire brain-case, apart from a narrow flange which projects from behind this covering. There are no unossified areas in the neurocranium itself. Fusion of the individual bones is almost complete and suture lines are consequently not easy to recognize.

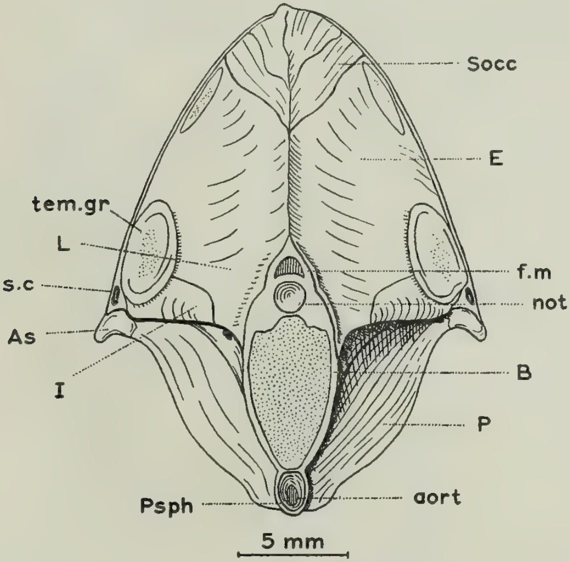

FIG. 38. *Dapedium* sp. Neurocranium, hind view, right side somewhat restored. From B.M.N.H. P 11189.

The postorbital portion of the neurocranium is the most difficult to interpret. However I agree with Woodward (1893, pl. 1, figs. 3 to 3*b*) and Frost (1913, fig. 2) that there is a well-defined supraoccipital forming the backwardly directed flange, and I cannot accept Rayner's suggestion that this is simply the two outstanding mesial edges of the epiotics (Text-fig. 38). The supraoccipital has a pronounced median crest projecting backwards for some distance. The epiotics and lateral occipitals make up the rest of the neurocranium in the postorbital region, but there is no distinct suture line separating them. The lateral occipitals form the border of the foramen magnum, and abut the intercalars ventrally. The demarcation of the intercalar is more pronounced and the true extent of this bone can be seen (Text-fig. 38). Just dorsal to the intercalars occur the temporal grooves. The lateral occipital continues round beneath the intercalars on to the lateral wall of the skull. In this region the tenth nerve emerged, the foramen for its exit being relatively large and directed backwards. Behind the tenth and nearer the foramen magnum is another small foramen which served for the exit of the occipital nerve (spinal nerve 1).

The basioccipital borders the notochordal pit, but it is the parasphenoid which forms the border of the ventral canal through which the dorsal aorta ran.

The major portion of the lateral wall of the neurocranium is made up of the prootic, which also covers the otic capsule (Text-fig. 39). In its dorsal region the prootic bears the hyomandibular facet, whilst just below this the position of the semicircular canals can be seen. Three clearly recognizable foramina are to be found in the prootic. The hindermost ones are for the exit of the ninth nerve. Of these two foramina the more posterior, smaller one transmitted the supratemporal branch of the ninth nerve, while the somewhat larger more anterior foramen transmitted the other branch. The two exits are separated by the external semicircular canals.

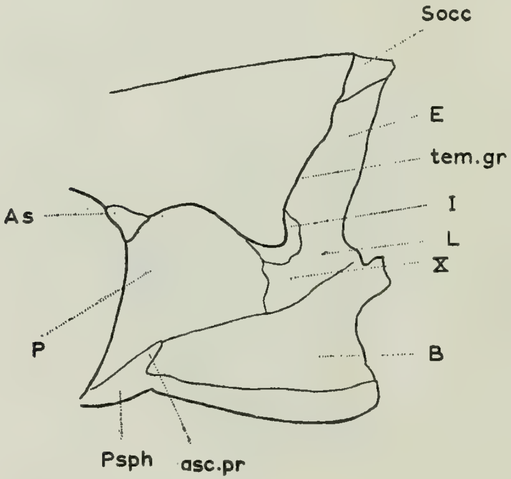

FIG. 39. *Dapedium* sp. Neurocranium, lateral view, slightly diagrammatic. After B.M.N.H. P 11189.

Again slightly to the anterior and just below the exit of the foremost branch of the ninth is a much larger foramen which served for the passage of the seventh nerve. The hyomandibular branch of the seventh must have passed straight down from this foramen into the hyomandibular bone, whilst the facial branch continued on and passed through the facial foramen into the orbit. There was no true trigemino-facial chamber, and in this respect *Dapedium* resembles its near relative *Lepidotes*.

The facial foramen is fairly large, and besides transmitting the buccal branch of the seventh it served for the passage of the jugular vein (Text-figs. 40 and 41). Running back from the facial foramen is a well-marked groove which continues across the surface of the prootic and the lateral occipital and was most probably for the reception of the jugular vein.

The autosphenotic is small in this species and again the suture line on the optic surface is indistinguishable. There is a small somewhat rounded basipterygoid process.

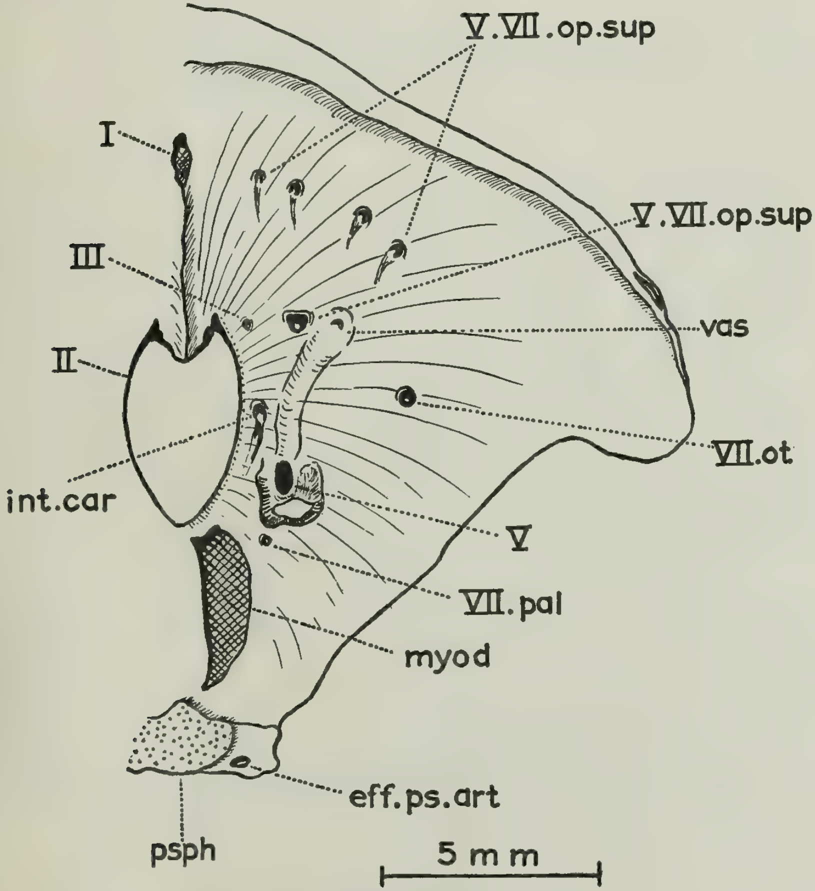

FIG. 40. *Dapedium* sp. Neurocranium as if cut vertically just anterior to the optic foramen, showing the left orbital surface. From B.M.N.H. P 11189.

The walls of the orbit, as pointed out by Rayner (1948 : 307) are not unlike those of *Lepidotes* and the infraorbital fenestra is fairly small. However, the fusion of the individual bones within the orbit is so complete that the demarcation of the pterosphenoid, autosphenoid and prootic cannot be seen. The basisphenoid is broken so that only a little of it remains, but the extent of the myodome on either side can still be made out.

All the foramina in the orbital surface are well defined and clearly recognizable. Immediately above the facial foramen, and partially let back into the roof of it so that it appears in a recess, is a larger foramen. From this issued the main branches (mandibular and maxillary) of the trigeminus. From the facial recess a groove ascends, finishing in a downwardly directed foramen. This appears to be vascular and served for the passage of a branch of the jugular vein into the neurocranium itself. Close to the side of this and towards the mid-line, is a larger foramen through which the superficial ophthalmic had its exit. Nearer to the mid-line again is a somewhat reduced opening which probably transmitted nerve III.

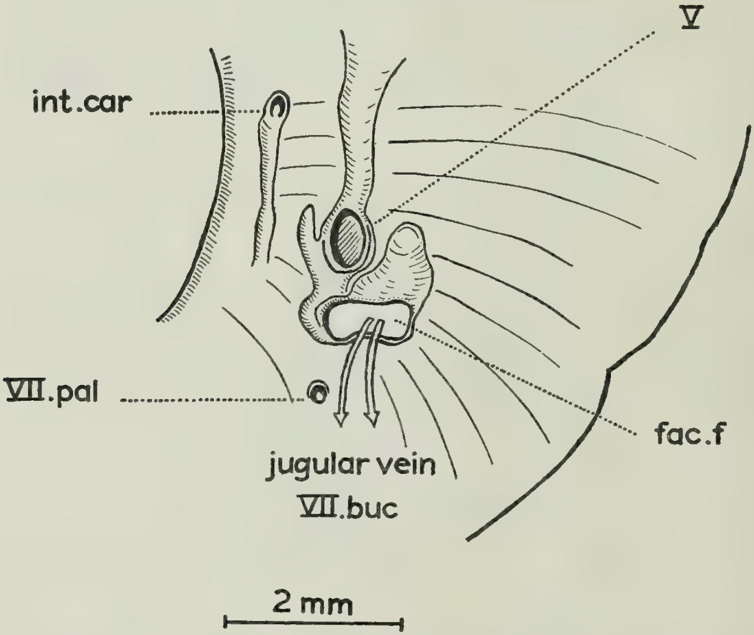

FIG. 41. *Dapedium* sp. Neurocranium as if cut vertically just anterior to the optic foramen, showing the basal portion of the left orbital surface. From B.M.N.H. P 11189.

Towards the roof of the orbit several foramina with downwardly directed grooves pierce the pterosphenoid. These were for secondary branches of the superficial ophthalmics, supplying sensory organs of the supraorbital canal.

The palatine branch of the seventh appears to have emerged through the small foramen which pierces the wall of the orbit just below the facial foramen, whilst a slit-like opening beneath nerve III probably transmitted the internal carotid artery.

The remaining foramen is more laterally situated than the rest, and from it the otic nerve emerged.

The two deep nasal pits are floored by the ethmoid and the posterior walls are pierced by a pair of foramina, through which the olfactory nerves ran. The parasphenoid in specimen No. 36705 from the Sedgwick Museum, Cambridge, bears a basipterygoid process ; at the base of this in specimen B.M.N.H. P 11189 is a small foramen which probably accommodated the efferent pseudobranchial artery.

An adequate description of the semicircular canal system has already been given by Rayner (1948 : 308).

Genus ***TETRAGONOLEPIS*** Bronn, 1830

1852. *Pleurolepis* Quenstedt, p. 214.
1860. *Homoeolepis* Wagner, p. 92.

Diagnosis. Trunk laterally compressed, deeply fusiform or cycloidal with the abdominal region protuberant ventrally. Head small in relation to body and the interopercular is deeper than the subopercular. Teeth styliform with a conical apex, those on the dentary forming a regular series, longer than those on the maxilla. Suborbitals three in number and there is a complete circlet of nine orbitals bordering the orbit. Cleithrum sigmoidal in outline, quite unlike the cleithrum in the allied genus *Dapedium*. There are only three branchiostegal rays and these are characteristically arranged, the first having an unusual shape, both the anterior and posterior edges being concave. The vertebral column consists of distinct pleuro- and hypocentra, and the neural spines are always fused with their supporting arches. Both the neural and haemal spines in the caudal region bear a laminar expansion at the base of their anterior borders. The paired fins are small and delicate, the pectorals arising at the level of the subopercular and the pelvics arising on the posterior edge of the protuberance. The dorsal fin is elongated as in *Dapedium* arising about the middle of the back, with the anal fin shorter and opposed to the hinder end of the dorsal. The caudal fin is not forked. All the lepidotrichia are distally segmented and bifurcated. The scales are quadrangular, very deep on the ventral portion of the body, but less deepened above the lateral line. Scales are smooth or feebly tuberculated with a much thickened anterior border which forms the peg-and-socket articulation. The ventral ridge scales are much larger than the dorsal, but both are serrated.

Type species. *Tetragonolepis semicincta* Bronn.

Tetragonolepis discus Egerton

(Text-figs. 42, 43)

1853. *Tetragonolepis discus* Egerton, p. 278, pl. 11, fig. 5.
1860. *Pleurolepis discus* (Egerton) Wagner, p. 96.
1895*b*. *Tetragonolepis discus* Egerton : Woodward, p. 160.

Diagnosis. A Tetragonolepid almost cycloidal in outline and with a less protuberant abdominal region. It is smaller than the type species and the scales are smooth apart from a series of concentric growth lines. The posterior margin of the scales is entire and not serrated.

LECTOHOLOTYPE. B.M.N.H. P 7625, the type nominated by Woodward (1895*b* : 160), from the Upper Lias, Gloucestershire.

MATERIAL. Specimens in the B.M.N.H. and the Royal Scottish Museum, Edinburgh.

DESCRIPTION. *The skull.* The skull roofing bones are feebly ornamented. The greatest degree of ornamentation is found on the suborbitals, which are covered by numerous tubercles of enamel. That on the extrascapulars, parietals and frontals is sparse, confined to a few isolated tubercles. The remaining skull bones appear smooth, in particular those constituting the opercular apparatus.

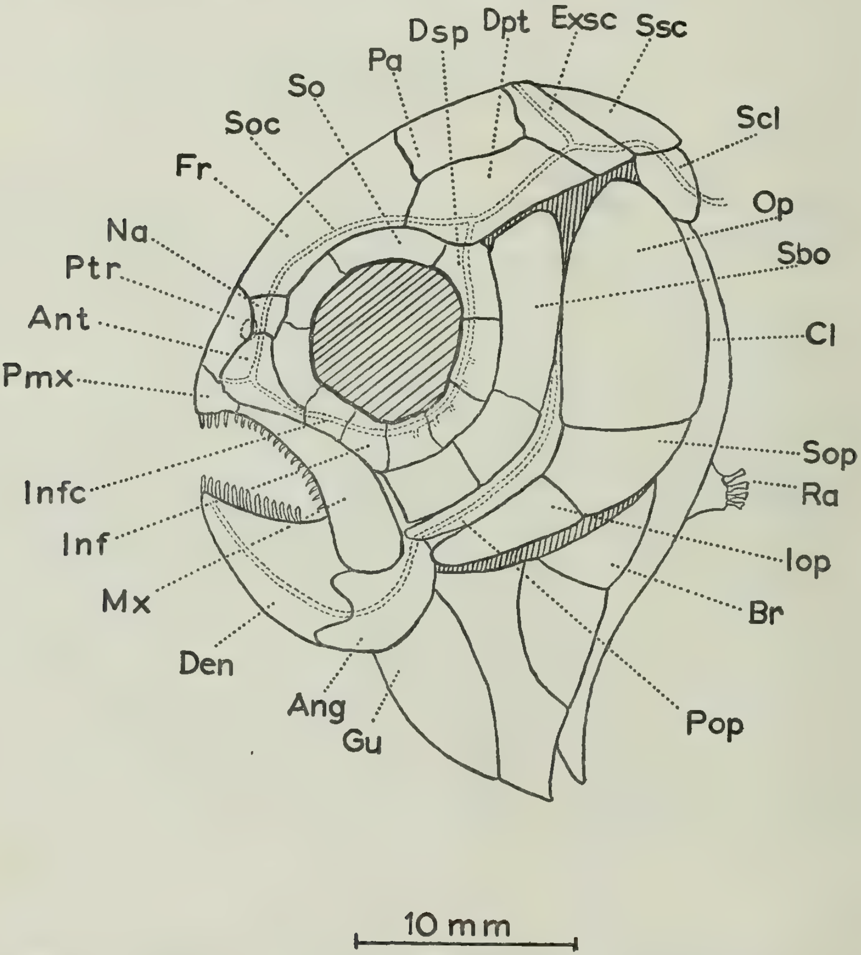

FIG. 42. *Tetragonolepis discus* Egerton. Restoration of skull in lateral view.

The skull roofing bones are invariably fused to one another making the suture lines difficult to decipher. The parietals are almost square in outline, bounded on either side by the larger dermopterotics (Text-fig. 42). The extrascapular is of the usual shape in contrast with the arrangement seen in *Dapedium* where a series of four or more bones occur in the corresponding position. Behind the extrascapular is the large suprascapular, to which the pectoral girdle articulates. Anteriorly the broad frontals abut the postrostral and the nasals. The whole region of the snout is difficult to interpret, and in order to appreciate the individual bones and their relationship it was necessary to supplement the material of *T. disca* by an examination of the allied species *T. semicincta*. The postrostral is larger than the nasal, spatulate in shape dorsally and narrowing as it runs forwards. The nasal is small and quadrangular, in contact with the postrostral anteriorly and the antorbital ventrally. The antorbital is triangular, articulating with the postrostral and premaxilla anteriorly and the maxilla ventrally. Whether or not external nares were present in this area could not be ascertained with certainty. The nasal, postrostral and antorbital are all discernible on one specimen of *T. semicincta*, R.S.M. 1877–30.3, while B.M.N.H. P 3625 of the same species displays the antorbital. Further, on B.M.N.H. P 1595 (*T. semicincta*) a postrostral element is apparent. The premaxilla is small and short, bearing some three or four teeth along its lateral edge (R.S.M. 1901–70.3, *T. discus*). The maxilla is longer and stouter with a spatulate expansion posteriorly. No trace of a supramaxilla was observed. The teeth on the maxilla are similar to those on the premaxilla and dentary but are somewhat smaller and do not continue right to the posterior end of the bone.

A complete ring of orbital plates surrounds the eye, nine in number including the dermosphenotic. Between the posterior infraorbitals and the opercular apparatus lie three suborbital bones. The most dorsal one is by far the largest and runs almost the full length of the opercular. The opercular is much larger than the subopercular and the whole apparatus forms an arched series.

Lower jaw. The lower jaw is almost identical with that of *Dapedium* and includes a dentary, angulo-articular and a toothed prearticular. The dentary bears only a marginal tooth row and the suture line between it and the angulo-articular follows a zig-zag course as in *Dapedium*.

Between the rami of the lower jaws is a large gular plate, this is followed by a series of three branchiostegal rays. The first branchiostegal ray has concave anterior and posterior edges, and behind it fit two further rays more triangular in shape. Both the gular plate and the rays are almost smooth with no noticeable tuberculations (B.M.N.H. P 7623).

Palate. The parasphenoid is narrow and does not appear to bear teeth. The quadrate is small articulating with a larger metapterygoid. The major portion of the palate is made up of the very deep ento- and ectopterygoids, together forming an extensive but thin sheet, stretching from the hinder end of the maxilla to the parasphenoid (R.S.M. 1901·70.3). The inner surfaces of these pterygoids are smooth and not dentigerous.

Hyoid arch. On no specimen of *T. discus* was this recognizable. However, on one specimen of *T. semicincta* (R.S.M. 1879·30.3), a ceratohyal is present. It is a stout ossification, narrow posteriorly but expanding considerably towards its anterior extremity.

Sensory canal system. The main cephalic division of the sensory canal runs through the ventral edge of the extrascapular, giving off the supratemporal commissure. It continues through the dermopterotic, dermosphenotic and round the infraorbital series as the infraorbital canal. Anteriorly it enters the antorbital where it divides, one half continuing forwards, presumably into the postrostral, while the other unites with the supraorbital canal in the nasal. The supraorbital canal passes upwards through the frontals and unites with the infraorbital canal in the dermopterotic. The preopercular canal is prominent, and passes into the lower jaw as the mandibular canal.

Appendicular skeleton. A small supracleithrum articulates the suprascapular to the cleithrum. The cleithrum itself continues downwards to almost the ventral border of the body. Ventrally the cleithrum curves backwards, giving the girdle an unmistakable sigmoidal flexure, not met with in *Dapedium.* At the level of the subopercular the ossified primary girdle supports four radials (B.M.N.H. P 3624). The fin is delicate and made up of approximately twelve lepidotrichia.

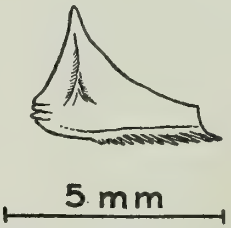

FIG. 43. *Tetragonolepis discus* Egerton. Ventral ridge scale. From B.M.N.H. P3624.

The pelvic girdle consists of two small bony rods articulating some seven or eight delicate lepidotrichia. The fin arises near the bottom of the ventral protuberance of the body, in a corresponding position to that in *Dapedium.*

Unpaired fins. The dorsal fin stretches from the dorsal apex of the body almost to the tail, and like the somewhat shorter anal fin has the same number of endoskeletal supports as lepidotrichia. The caudal fin is not forked and in *T. semicincta* has eight haemal spines supporting the lower lobe (R.S.M. 1901·70.2).

Axial skeleton. The vertebral column consists of distinct pleuro- and hypocentra. The neural spines are fused to the supporting arches, and in the anterior portion of the body, that is in front of the dorsal fin, extend to the body margin. The haemal spines are shorter and do not reach the ventral border, but both these and the neural spines in the posterior region bear a small laminar expansion at the base of their anterior borders. There are no intermuscular bones.

Squamation. The scales, unlike that condition seen in *Dapedium*, have a sharply thickened rib on the inner face of their anterior borders. This forms the peg-and-socket articulation. The scales are quadrangular in shape and very deep on the ventral portion of the body, there being only five scales between the ventral margin and the lateral line. Above the lateral line there are some eight or ten scales, these are much smaller and nothing like as deep. Both the dorsal and ventral ridge scales are delicately serrated (Text-fig. 43).

Genus ***LEPIDOTES*** Agassiz, 1832

DIAGNOSIS. See Woodward, 1895*b* : 77 ; 1916 : 26.

TYPE SPECIES. *Lepidotes elvensis* (Blainville).

Lepidotes mantelli Agassiz

(Text-figs. 44, 45, 47)

1826. Figures of marginal teeth, Webster, pl. 6, figs. 5, 6.
1827. Scales, Mantell, p. 58, pl. 5, figs. 3, 4, 15, 16.
1833. (?) *Lepidotus subdenticulatus* Agassiz, **2**, pt. 1, p. 9, pl. 30, figs. 4–6.
1833. *Lepidotus mantelli* Agassiz, **2**, pt. 1, p. 9, pl. 30, figs. 10–15 ; pl. 30*c*, figs. 1–7.
1835. *Lepidotus fittoni* Agassiz, **2**, pt. 1, p. 265, pls. 30*a*, 30*b*.
1836. *Tetragonolepis mastodonteus* Agassiz, **2**, pt. 1, p. 216, pl. 23*e*, figs. 3, 4.
1841. *Lepidotus mantelli* Agassiz : Owen, p. 69, pl. 30, fig. 1 ; pl. 31.
1849. *Lepidotus mantelli* Agassiz : Williamson, p. 444.
1854. *Aechmodus mastodonteus* (Agassiz) Morris, p. 317.
1854. *Lepidotus fittoni* Agassiz : Morris, p. 331.
1854. *Lepidotus mantelli* Agassiz : Morris, p. 332.
1860. *Lepidotus fittoni* Agassiz : Lee, p. 458, pl. 12.
1887. *Lepidotus mantelli* Agassiz : Branco, p. 345, pl. 3, figs. 1, 2.
1890. *Lepidotus mantelli* Agassiz : Woodward & Sherborn, p. 112.
1895*b*. *Lepidotus mantelli* Agassiz : Woodward, p. 108, text-figs. 23, 24.
1896. *Lepidotus mantelli* Agassiz : Scupin, p. 162, pl. 9, fig. 8..
1908. *Lepidotus mantelli* Agassiz : Lankester, p. 79, text-fig. 46.
1916. *Lepidotus mantelli* Agassiz : Woodward, p. 36, pl. 7, fig. 7 ; pl. 8, figs. 1–4 ; pl. 9 ; pl. 10, figs. 1–3 ; text-figs. 16–18.

DIAGNOSIS. See Woodward, 1895*b* : 109 ; 1916 : 36.

LECTOTYPE. B.M.(N.H.) 2456 from the Wealden, Heathfield, Sussex, nominated as the type by Woodward (1895*b* : 109).

MATERIAL. Specimens in the Leicester Museum and Brit. Mus. (N.H.), from the Wealden of Sussex.

REMARKS. The neurocranium of this genus has received much previous attention. Woodward first described that of *Lepidotes latifrons* (1893 : 560) and later that of *Lepidotes mantelli* and another species of *Lepidotes* (1916, pl. 10, text-figs. 15, 16). More recently Holmgren & Stensiö (1936, fig. 364) described the neurocranium of *Lepidotes semiserratus*, and the same species is dealt with by Rayner (1948 : 305). Beltan (1957) described a neurocranium of the genus *Lepidotes* from the Bathonian of Morocco, which he assigns to the species *L. mantelli*. Apart from the fact that his specimen comes from the Lower Jurassic and that the earliest members recorded for *L. mantelli* are Wealden, the ossification of the neurocranium is very incomplete and in this respect it resembles *Lepidotes semiserratus* far more closely than it does *L. mantelli*. However, I found in the Leicester Museum a complete neurocranium and associated palate of *Lepidotes mantelli* from the Hastings Sands, Tilgate (Leicester Museum No. O.S. 5′ 1957), which after preparation has yielded sufficient information to make a redescription necessary.

Further, two isolated prootics of *Lepidotes latifrons* (B.M.N.H. P 9998) from the Oxford Clay at Peterborough have been cleaned up in acid, and confirmation of all the existing foramina in the prootic of *Lepidotes mantelli* obtained.

Description. *Neurocranium.* This is well ossified. All the bones constituting the neurocranium are stout and cancerous, together forming a much more solid and heavy brain-case than in *Lepidotes semiserratus* (Rayner, 1948 : 305). The large prootics which have grown back over the lateral and basioccipitals have eliminated most of the cartilaginous interspaces seen in earlier species.

The epiotics are large and meet in the mid-line. Posteriorly they present a triangular appearance forming over half of the depth of the occiput, and there is no supraoccipital. Beneath the epiotics lie the even larger lateral occipitals which, meeting in the mid-line, extend ventrally to form the upper rim of the foramen magnum. The lateral occipitals extend a considerable distance on to the lateral wall of the neurocranium, completely surrounding the foramen for the vagal nerve (Text-fig. 44). Dorsally abutting on the lateral occipital and not quite reaching the anterior edge of the epiotic is a small intercalar (opisthotic of Woodward, 1916, pl. 10, fig. 1).

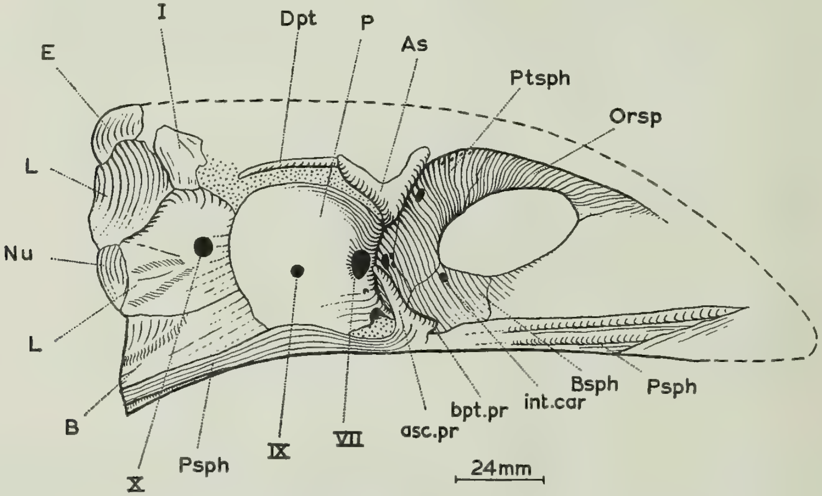

Fig. 44. *Lepidotes mantelli* Agassiz. Neurocranium in lateral view, slightly diagrammatic. From Leicester Museum O.S. 5, 1957.

Beneath the lateral occipital is a massive basioccipital which is capped posteriorly by a pair of neural arches. The basioccipital is distinctly grooved below for the basicranial canal.

The prootic is another large element which posteriorly meets both the basioccipital and the lateral occipital, but which is separated from the intercalar by a cartilaginous interspace. Dorsally there is a narrow unossified space between the prootic and the dermopterotic. The hyomandibular has its articulatory facet up on the underside of the projecting dermopterotic. The lateral wall of the prootic is pierced by the glossopharyngeal and facial foramina. The antero-ventral corner of the prootic is unossified and there is a distinct notch marking the entry of the internal carotid artery. The bones of the orbital surface are distinct and the foramina obvious (Text-figs. 44–46).

The myodome is small but the basisphenoid is of the same massive proportion as in *Lepidotes semiserratus* (Rayner, 1948, fig. 12). A downwardly directed foramen near the upper margin of the basisphenoid was clearly for the entry of the internal carotid.

There is a distinct gap between the ascending process of the parasphenoid and the edge of the prootic (not shown in Text-fig. 45) and it is probable that it served for the passage of the jugular vein into the orbit (see Text-fig. 44).

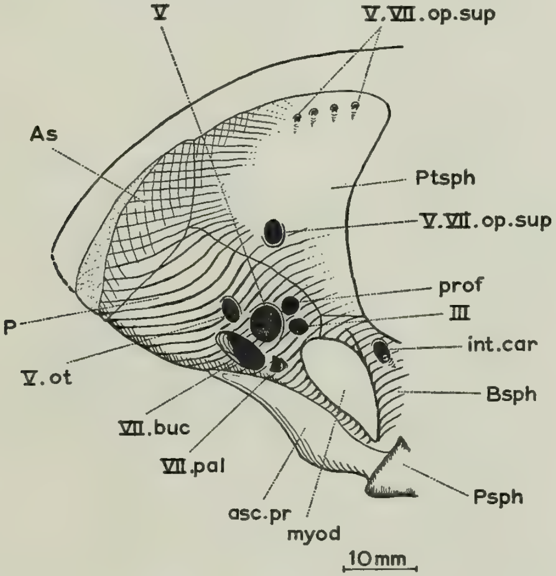

Fig. 45. *Lepidotes mantelli* Agassiz. Neurocranium as if cut vertically just anterior to the optic foramen, showing the right orbital surface. From Leicester Museum O.S. 5, 1957.

The facial foramen is set back in the bone and the passages of its various components can be clearly demonstrated in the isolated prootic of *Lepidotes latifrons* (B.M.N.H. P 9998). The hyomandibular branch passes back out on to the lateral wall of the prootic, whilst the largest foramen opening into the orbital surface transmitted the buccal branch of the facial. Immediately below this foramen is a much smaller and downwardly directed foramen through which passed the palatine branch. Dorsally to the facial foramen and nearer the mid-line is another large somewhat recessed foramen which served for the exit of the trigeminus. Above and between the facial and trigeminal foramina is a smaller foramen for the otic branch of the facial. Nearer the mid-line again from the trigeminal foramen and still within the boundary of the prootic are two further foramina, the more dorsal transmitted the profundus, while the larger ventral one served for the passage of the occulomotor nerve. The remaining recognizable foramen in the prootic is small and occurs in the groove beneath the foramen of the palatine branch of the facial. It probably transmitted the abducens nerve during life (Text-fig. 46).

The pterosphenoid has an upwardly directed foramen next to its lower boundary that marks the exit of both the superficial ophthalmic nerves; several passages piercing the upper region of the same bone are for the secondary branches inervating the supraorbital canal. The bony infraorbital septum is perforated by an infraorbital fenestra with which the optic foramen is confluent. In the ethmoidal region the olfactory nerves are invested in bone, the true homologues of which are uncertain.

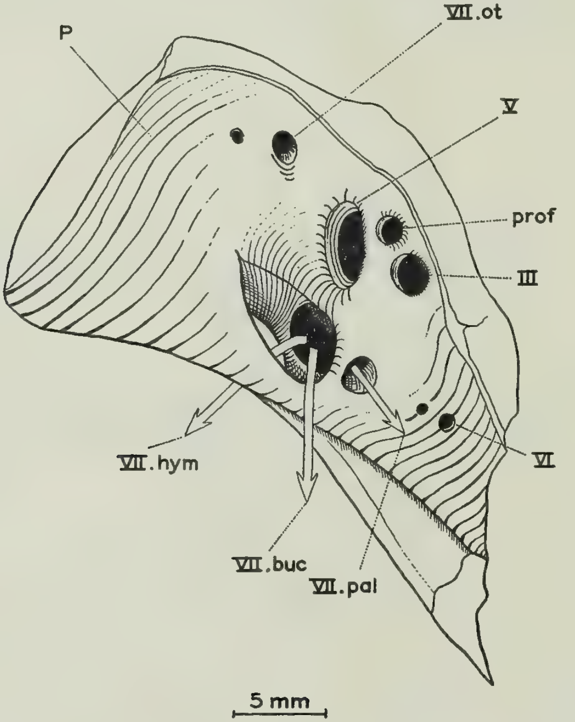

FIG. 46. *Lepidotes latifrons* Woodward. Right prootic viewed from the orbital surface. From B.M.N.H. P 9998.

The parasphenoid curves sharply downwards posteriorly and the distinction between the ascending and basipterygoid processes is slight. There is no rounded notch in front of the basipterygoid process as described by Rayner (1948 : 306) in *Lepidotes latrifrons*.

The neurocranium of *L. mantelli* is very similar in make up to that of the related Semionotid, *Dapedium* (p. 300). In *Dapedium* the same number of bones form the lateral wall of the neurocranium and the relationships of the nerve foramina to the bones are essentially the same. The foramen for the exit of the hyomandibular and buccal components of the seventh nerve is situated in the lateral wall posterior to the orbit in both *Dapedium* and *Lepidotes*. Two important differences are the presence of an aortic canal in *Dapedium*, absent in *Lepidotes*, and the presence in *Dapedium* of a bone filling the posterior-dorsal angle in the back of the skull, which I have termed the supraoccipital although it is probable that this bone is not homologous with the supraoccipital of other Holosteans. Both forms have a small intercalar and an extensive lateral occipital and in neither is there an opisthotic present.

Palate. The palate of *Lepidotes semiserratus* has been described by Rayner (1948, fig. 10). However, that of *Lepidotes mantelli* differs in a few respects sufficient to warrant a description (Text-fig. 47).

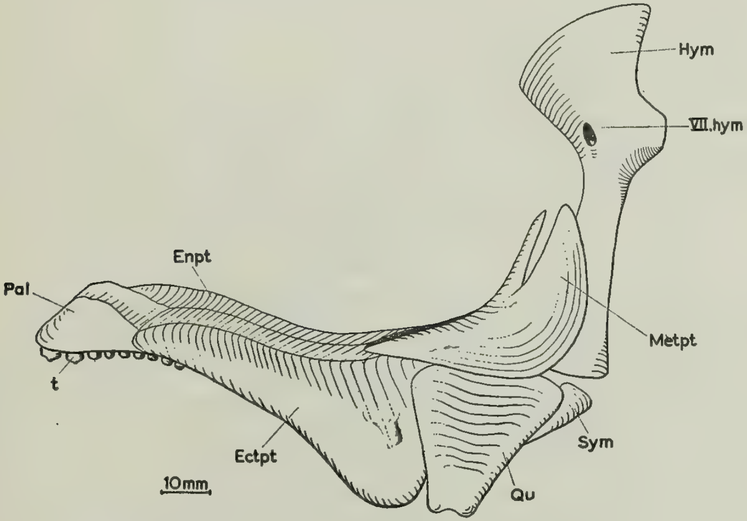

Fig. 47. *Lepidotes mantelli* Agassiz. Reconstruction of the left palate. From Leicester Museum O.S. 5, 1957.

The mandibular suspensorium is only slightly inclined forward and the hyomandibular is stout with a posterior projection for the support of the opercular bone. The metapterygoid is an extensive ovoid-shaped bone with a V-shaped notch in its posterior border. This bone is distinctly flattened in a horizontal plane, but curves sharply upwards posteriorly. Its inner edge articulates for a short distance with the basipterygoid process and it is probable that the outermost posterior flange fitted over the ventral portion of the hyomandibular. The quadrate is stout and there is a small symplectic between it and the hyomandibular. The ectopterygoid is the largest bone in the palate and forms with the entopterygoid a broad ledge running out from the parasphenoid in a more or less horizontal plane. The ectopterygoid then turns downwards almost through a right angle to constitute the outer edge of the palate. The entopterygoid itself is a narrow strip of bone filling the gap between the parasphenoid and the ectopterygoid. Woodward (1916, fig. 16) figures a transverse section of the palate of *Lepidotes mantelli* and from this the extent of the entopterygoid and ectopterygoid can be seen. Anteriorly the ectopterygoid bears teeth and in front of it and often fused indistinguishably with it is the stout tooth-bearing palatine. Between the palatines and pterygoids of either side is a large vomer, also bearing teeth.

Family LEPTOLEPIDAE

DIAGNOSIS. See Woodward, 1895*b* : 500.

Genus ***LEPTOLEPIS*** Agassiz, 1832

1839. *Ascalabos* von Münster, p. 112.
1848. *Tharsis* Giebel, p. 145.
1850. *Sarginites* Costa, p. 285.
1850. *Megastoma* Costa, p. 287.

DIAGNOSIS. See Woodward, 1895*b* : 501.

TYPE SPECIES. *Leptolepis coryphaenoides* (Bronn).

Leptolepis africana sp. nov.

(Text-fig. 48)

DIAGNOSIS. Much smaller than the type species not exceeding 5 cm. in length, of which the head and opercular apparatus constitute approximately 1·3 cm. The suture between the frontals is almost a straight line with nothing like the wavy nature seen in *Leptolepis coryphaenoides*. The supramaxillaries are appreciably deeper than the maxilla and together form a comparatively greater sheet of bone than in the type species. The ornamentation of the supramaxillaries is characteristic, consisting of diagonal wavy ridges of enamel running antero-dorsally, postero-ventrally, whilst the diagonal ridges of enamel on the maxilla run postero-dorsally, antero-ventrally. The scales are cycloidal, ornamented with concentric rings of enamel.

HOLOTYPE. B.M.N.H. P 38526 and counterpart P 38527 from the Trias? of Mandawa, Tanganyika.

MATERIAL. The unique holotype, comprising head and two-thirds of the body.

REMARKS. This is the first record of the genus *Leptolepis* occurring in East Africa. The earliest known members of this genus have generally been regarded as of Upper Liassic age. However, there is one specimen of *Leptolepis* of undoubted Triassic age known to the author, which is in Professor D. M. S. Watson's collection and this comes from Seefeld, Austria. The holotype here described was discovered in a boring put down by the B.P./Shell Petroleum Development Co. of Tanganyika Ltd. at Mandawa, Tanganyika, and generously presented by them to the Department of Palaeontology of the British Museum (Natural History). The co-ordinates of this Mandawa Well are: 9° 24′ 58″, 4 S. and 39° 25′ 3″, 7 E., and the specimen of *Leptolepis africana* was discovered at a depth of 10,520 ft. It seems possible that the age of the bed containing the holotype could be from Upper Triassic to Lower Liassic and it is hoped that accurate dating will be forthcoming in the near future.

DESCRIPTION. *The skull.* The external bones of the skull are covered by a very thin layer of enamel. The majority of the bones are smooth, but the maxilla and supramaxillaries exhibit a characteristic ornamentation. On the supramaxillaries the ornamentation takes the form of a few wavy ridges running antero-dorsally, postero-ventrally. On the maxilla the ridges are confined to the central position where they run in the reverse direction, viz. postero-dorsally, antero-ventrally.

The frontals are by far the largest bones of the skull roof, broad behind but narrowing sharply between the orbits. The suture line between these much elongated frontals is almost straight, and does not exhibit the sinuosity seen in the type species. Anteriorly the edges of the frontals are even narrower, being scalloped out for the reception of the nasal bone. Both the frontal and nasal bones abut on to the rostral. The rostral is a small ossification and forms the lower border of the nasal orifice, the nasal itself forming the upper boundary. There is some evidence of a further bone between the nasal and the orbit, and it is reasonable to suppose that there was an antorbital present in that position. The parietals are small and square with a larger dermopterotic making up the remainder of the lateral border of the skull roof. Behind the parietal is the extrascapular and a much enlarged suprascapular. The suprascapular is relatively larger than that seen in *Leptolepis*

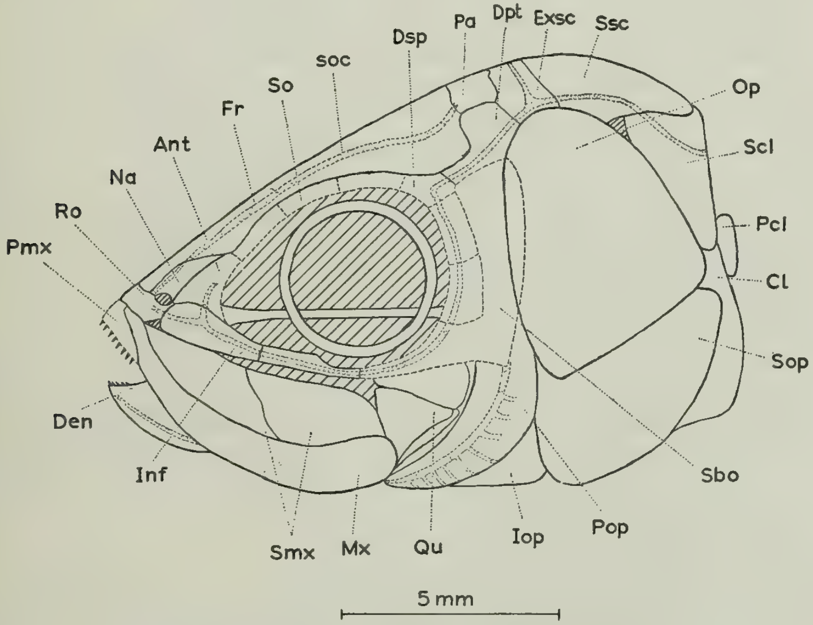

FIG. 48. *Leptolepis africana* sp. nov. Restoration of skull in lateral view.

coryphaenoides and more reminiscent of the suprascapular in *Pholidophorus similis*. Of the supraorbital and infraorbital series of bones, little can be made out. Anteriorly, however, adjoining the antorbital and rostral bones above, and the anterior supramaxilla beneath, is a large spatulate-shaped ossification which is the most anterior member of the infraorbital series. It narrows somewhat posteriorly where it meets the next member of the infraorbital series. These two bones together form a bar beneath the orbit.

The maxilla is long and curved, deepening somewhat at its posterior extremity. The lower border of the maxilla is convex except at its anterior extremity where it becomes concave for the reception of the small premaxilla. Above the maxilla are two elongated supramaxillaries of approximately the same size. These overlap the maxilla to a certain extent. No teeth were recognizable on the maxilla.

Of the lower jaw little can be made out, but the opercular apparatus seems identical with that of *Leptolepis coryphaenoides*. The state of preservation is too poor to make out other structures such as a sclerotic ring, palate, etc.

Appendicular skeleton. The pectoral girdle is a stout ossification. The supracleithrum is a long blade-shaped bone, broadest dorsally and carrying the hindermost portion of the main lateral line canal. The cleithrum is much thickened ventrally, especially where it articulates with the primary portion of the pectoral girdle. The membrane bones of the primary girdle are ossified as in the later, Liassic species. A delicate postcleithrum is also present.

The pectoral fin consists of some sixteen to twenty lepidotrichia, which are not jointed proximally.

The pelvic girdle consists of two triangular-shaped bones, with thickened lateral borders. The insertion is narrow, there are no supporting radials and the innermost fin-ray has no enlarged basal portion for the articulation of neighbouring rays, as described by Rayner (1937 : 67) in *Leptolepis coryphaenoides*. Instead the base of the stoutest outermost fin-ray is curved inwards to function probably as support for at least the next two succeeding lepidotrichia.

The lepidotrichia of the pelvic fin number between thirteen and fifteen.

Unpaired fins. The dorsal fin arises at almost the same level as the pelvic fins, but the number of fin-rays present in both it and in the anal could not be counted accurately. Both are supported by radials. The caudal fin is missing from the specimen.

Axial skeleton. The vertebrae, ribs and intermuscular bones are all similar to that described by Rayner (1937 : 68) in *Leptolepis coryphaenoides*.

Squamation. The body is covered in cycloidal scales, all delicately ornamented with concentric rings of enamel.

Scale Structure of Pholidophorus and Leptolepis

The evolution of the Teleosts from the Pholidophorid-Leptolepid line has been demonstrated by Rayner (1934, 1938) and Saint-Seine (1949*a*) on gross structure.

One of the most marked characteristics of the Teleosts is the structure of their scales. The scales of typical Teleosts are cycloidal and composed of several thin layers of bone (lamellae). Within these bony layers there are no cells and no structures such as blood vessels or tubules of any description. This type of scale without enclosed cells is a highly specialized structure that must have evolved from the normal cell-bearing bone of the scale of more primitive Actinopterygians (Klaatsch, 1890; Reis, 1895; Stephan, 1900; Goodrich, 1913; Voigt, 1934; Ørvig, 1951, 1957; Bernhauser, 1954). According to Reis (1895 : 163) the more primitive Teleosts such as the Elopidae, Characinidae and Salmonidae possess a scale which, like that of their " Ganoid " ancestors, is rich in normal bone cells. In the more specialized Teleosts these cells have disappeared, not only from the scales, but from the dermal bones.

The typical " Palaeoniscid " scale (Williamson, 1894; Scupin, 1896; Goodrich, 1907, 1913; Stensiö, 1932; Gross, 1935, 1947; Aldinger, 1937; Ørvig, 1951, 1957) consists of three layers, an outermost layer of enamel, beneath it a layer of dentine and basally a thicker layer of bone. Entering the scale from the basal face and ascending towards the dentine layer are numerous canals of Williamson (Ørvig, 1951 : 362). These vascular canals connect with the dentinal tubules which form a close network just below the enamel. The dentinal tubules secrete the layer of dentine. Throughout the bony tissues are numerous cell spaces.

From the " Palaeoniscoid " type of scale develops the " Lepidosteoid " type (Goodrich, 1913 : 758) which is characteristic of the majority of Holostei. In the " Lepidosteoid " type of scale the dentine layer has disappeared together with the dential tubules, and the canals of Williamson although present have lost their contained blood vessels and become functionless. However, there are still numerous cell spaces throughout the bony tissue.

Ørvig (1957 : 487) has shown in certain Palaeonisciformes how the reduction of cells in the bony tissues could have come about. In the Subholostean *Perleidus stoschiensis* Stensiö from the Lower Lias of East Greenland, the bone cells have assumed a somewhat unequal distribution by the concentration of some of them near the canals of Williamson. A more advanced stage occurs in the Palaeoniscid *Scanilepis dubia* (Woodward) from the Rhaetic beds of Scania, where all the bone cells of the hard tissue have become concentrated in the vicinity of the canals of Williamson. Finally, in the Palaeoniscid *Orvikuina vardiaensis* Gross from the Baltic Upper Middle Devonian, the canals have lost their original vascular function and the bone cells have become withdrawn into their interior. This series is, of course, stratigraphically in reverse.

Pholidophorus higginsi Egerton (Text-fig. 49)

The genus *Pholidophorus* ranges from the Upper Trias to the Upper Jurassic (Purbeckian), *Pholidophorus higginsi* being one of the first species of the genus to appear. The specimen sectioned, B.M.N.H. 41279, came from the Rhaetic of Aust. The scales are thick, rhombic and deeply imbricating, with their hinder margins often somewhat rounded.

Microstructure. The structure of the scale can be seen from Text-fig. 49 and is similar to that type of scale termed " Lepidosteoid " by Goodrich (1907 : 758).

There is a thick outer layer of enamel (ganoine) on the surface with a much thicker bony layer beneath. The basal bone tissue contains large cell spaces, and is penetrated by numerous, fairly thick, canals of Williamson. These canals ascend more or less vertically from the basal face of the scale, terminating just below the enamel.

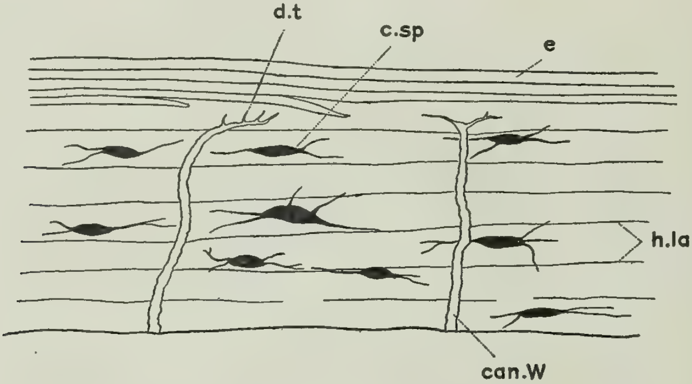

FIG. 49. *Pholidophorus higginsi* Egerton. Vertical section of scale. From B.M.N H. 41279, × 250 approx.

Pholidophorus caudalis Woodward (Text-fig. 50)

This second species of *Pholidophorus*, *P. caudalis*, was selected because it occurs later geologically, and has scales very different from those of the Rhaetic form. They are generally thinner, although still deeply imbricating. The specimen sectioned came from the Lower Lias of Lyme Regis, B.M.N.H. P 939*a*.

Microstructure. The scale is much thinner and the layer of enamel quite thin. The significant difference between this species and *P. higginsi* is the complete absence of recognizable cell spaces in *P. caudalis* (Text-fig. 50). The cells have already been withdrawn from the bone tissue. The canals of Williamson no longer appear vascular, and are very few in number. Whether or not these few remaining canals of Williamson contained the missing bone cells from the surrounding bone tissue could not be ascertained.

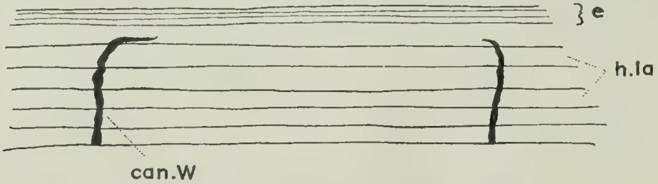

FIG. 50. *Pholidophorus caudalis* Woodward. Transverse section of scale. From B.M.N.H. P 939*a*, × 200 approx.

Leptolepis concentrica Egerton

The scales of this genus are no longer rhomboidal, but resemble more closely those of the Teleostei. They are cycloidal, very thin and with only a trace of a layer of enamel on them. They are also deeply imbricating. The specimen sectioned came from the Lower Lias of Lyme Regis, B.M.N.H. P 3666.

Microstructure. The surface is covered in an extremely thin layer of enamel, with a thin bony layer beneath. There are no cell spaces recognizable, and no canals of Williamson.

Comments. Thus, within the genus *Pholidophorus* the reduction in the cells of the bony layer can be observed. The Rhaetic species *P. higginsi* shows a normal distribution of cells, whilst the later Liassic species *P. caudalis*, shows an almost complete absence of them. Further, the canals of Williamson, which are no longer needed now that the dentine layer has disappeared, also show reduction within the genus ; *P. higginsi* has a plentiful supply, whereas in *P. caudalis* there are very few.

In *Leptolepis* these changes are carried further, with the complete disappearance of the canals of Williamson and also of the cells of the bony layer. Apart from the thin layer of enamel the scales of *Leptolepis* are perfectly normal Teleostean scales.

If we assume that the bony cells once lost cannot be re-acquired, as would be expected in view of the general, though not invariable, irreversibility of evolutionary process, then it is clear that the Elopidae, Cyprinoidea and Salmonidae must have separated off from the main Teleost stock at the *Pholidophorus* level of evolution and that *Leptolepis* cannot be ancestral to them.

Family Pycnodontidae

Diagnosis. Trunk much laterally compressed, discoidal or very deeply fusiform. External skull bones robust, with a median supraoccipital plate separating the parietals. Cheek bones very rarely present. Where they occur they are thin and delicate. Mandibular suspension inclined well forwards, gape small. Dentition : teeth prehensile on the premaxilla and dentary, and tritoral on the vomer and splenials. Opercular apparatus distinctive, with a small opercular and a much enlarged preopercular. Never more than a much reduced series of branchiostegal rays. No ossification in the notochordal sheath, lepidotrichia stout, well spaced and articulated. The lepidotrichia equal their supporting radials. Fulcra generally absent. Dorsal and anal fins extended and have long insertions. The scales are rhombic with well-marked peg-and-socket articulations. Squamation often confined to the anterior region. Tail hemiheterocercal.

Genus **EOMESODON** Woodward, 1918

Diagnosis. Profile of head especially steep, and abdominal region of the trunk deepened. Caudal region relatively small. Not less than three outer series of splenial teeth.

Type species. *Eomesodon liassicus* (Egerton).

Eomesodon liassicus (Egerton)

(Text-figs. 51–54)

1854. *Pycnodus liassicus* Egerton, p. 436.
1855. *Pycnodus liassicus* Egerton : Egerton, no. 10, pl. 10.
1856. *Mesodon liassicus* (Egerton) Heckel, p. 202.
1895*b*. *Mesodon liassicus* (Egerton) : Woodward, p. 202.
1917. *Mesodon liassicus* (Egerton) : Woodward, p. 388.
1918. *Eomesodon liassicus* (Egerton) Woodward, p. 54, fig. 21.
1949*b*. *Eomesodon liassicus* (Egerton) : Saint-Seine, p. 334, fig. 1.

Diagnosis. An *Eomesodon* with only one of the principal vomerine teeth coarsely crimped or tuberculated round the apex of the crown. Ornamentation of the skull roofing bones and the scales consists of closely arranged, large, flattened tubercles. In the caudal region each neural spine beneath the dorsal fin is double, and the number of lepidotrichia in the dorsal and anal fins less than in the typical *Mesodon*.

Holotype. Imperfect fish in the B.M.N.H. 19864, from the Lower Lias, Barrow-on-Soar, Leicestershire.

Material. Specimens in the B.M.N.H. and Worcester Museum.

Remarks. This species was first described by Egerton (1854 : 436) and is known from only four specimens. Two of these are the part and counterpart of the same fossil, one half being in the British Museum, P 1336, and the other in the Worcester Museum. Woodward (1895*b* : 203) has given the locality for P 1336 as the Lower Lias, Tarn Hill, Tewkesbury, Gloucestershire. However, on checking this locality on the Ordnance Survey map, I find that he has misinterpreted the original label, and the true locality should be Sarn Hill, Bushley, Gloucestershire.

Description. In general profile the head of *Eomesodon liassicus* is very steep. The anterior region of the trunk is elevated dorsally and the abdominal region much deepened. The tail is smaller than in the genus *Mesodon* and the squamation is complete over the whole of the trunk in advance of the median fins.

The skull. The skull, with a small median supraoccipital, is very similar in pattern to that of the typical Pycnodonts (Text-fig. 51). The cranial roof is ornamented with regular longitudinal rows of tubercles, often with striation between the rows. On the preopercular and the opercular the rows of tubercles follow the length of the bone.

On each side of the median supraoccipital is a large parietal. This bone is roughly rectangular in shape but with a blunt point anteriorly, reaching to the border of the orbit. From the course of the sensory canals along the posterior border of this bone I think that this is a compound ossification incorporating the parietal and extrascapular (or the post-temporal of Traquair, 1879, pl. 4; White, 1932: 82). The digitate prominence behind the parietal (X of Woodward, 1918, pl. 14, fig. 4) seen on many of the other Pycnodonts, possibly represents the vestiges of the suprascapular. This prominence has not been observed on any of the four specimens of this species, because the preservation in that area is poor. Beneath the parietal is a large dermopterotic (supratemporal—intertemporal of earlier workers) which borders the parietal ventrally. It is a deep four-sided plate tapering sharply forward above the orbit and forming part of its border. Posteriorly it has a long free border under which the supracleithrum lies. Beneath the dermopterotic is a much smaller rectangular plate separating it from the opercular and preopercular proper. This plate clearly belongs to the preopercular series since a continuation of the main preopercular canal runs through its anterior edge. In this respect *Eomesodon* resembles *Bobasatrania* and some of the Platysomids.

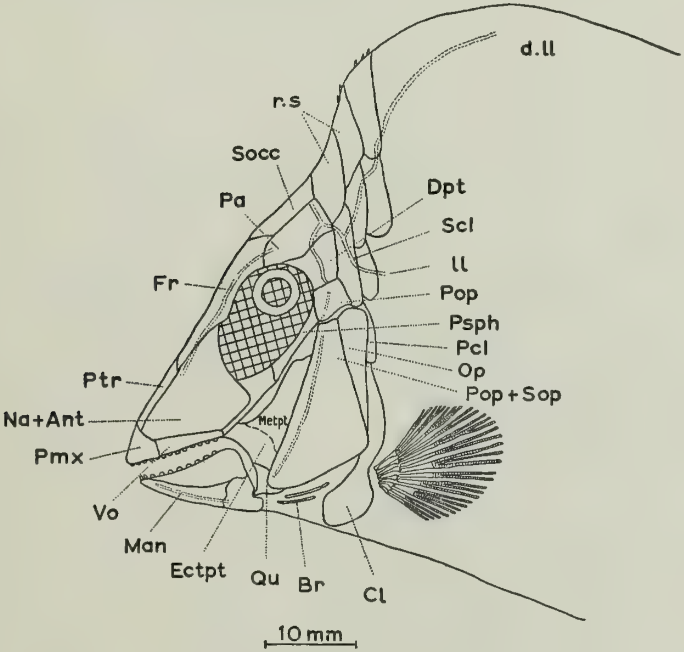

FIG. 51. *Eomesodon liassicus* (Egerton). Restoration of skull in lateral view.

The skull roof in front of the supraoccipital is composed of a pair of large frontals which are the largest bones of the skull. Traces of the sensory canal can be seen on them. They are expanded posteriorly, forming the antero-dorsal border of the orbits; and anteriorly they taper to meet another ossification which I have called the postrostral. Anteriorly the postrostral reaches the paired premaxillae. These are not complete on any of the specimens, but an impression of one can be seen on B.M.N.H. P 1336. The premaxilla is a small bone and it appears to have borne teeth. In front of the orbit there is only one large plate on either side, termed the mesethmoid by Woodward (1917 : 386). This so-called mesethmoid is a composite bone probably representing both the nasal and the antorbital. It is a stout thick bone, triangular in shape, and limits the orbit anteriorly. It is bounded below by the parasphenoid and the vomer. The supraorbital canal runs into the dorsal corner of the nasalo-antorbital, but its subsequent passage was not evident.

The parasphenoid extends forwards to the posterior corner of the nasalo-antorbital where it joins the single vomer. It is relatively stout anteriorly, but narrows beneath the orbit. The vomer is widened to support the stout dentition, and it projects beneath the ventral border of the nasalo-antorbital. The teeth on the vomer are mainly smooth with the principal tooth coarsely crimped or tuberculated round the apex of the crown (Egerton, 1854 : 436, B.M.N.H. 19864). There is evidence of an ossified sclerotic ring, but no cheek plates were observed. The preopercular is large and triangular with a much reduced opercular along its dorso-posterior border. The preopercular possibly represents a fusion of two bones, the preopercular and the subopercular.

The mandibular suspensorium is inclined forwards, with the ventral end of the hyomandibular in front of its dorsal end. Traces of the hyomandibular can be seen on B.M.N.H. P 1336 and there does not appear to be any anterior expansion to support the opercular. Ventrally there is a gap between the hyomandibular and the quadrate where the symplectic must have fitted. This is borne out by the presence of a distinct notch in that region of the quadrate. The quadrate is distinctly triangular with an articulatory surface ventrally ; this fits neatly into the corresponding facet in the angular of the lower jaw.

Lower jaw. The lower jaw is composed of three ossified elements only : the splenial, the dentary and the angular (Text-fig. 52). The splenial forms the greatest part of the mandibular ramus and bears most of the teeth, with the thinner dentary flanking it. The angular forms the posterior termination of the jaw, and the articulation with the quadrate. The splenial teeth are smooth and not indented, and there are not less than three outer series (cf. B.M.N.H. 35577). The dentary bears only two, somewhat chisel-shaped teeth with the outer one the larger. The teeth on the splenial are shorter and broader.

Beneath the preopercular are two fragments of bone which may represent the vestiges of the branchiostegal system.

Palate. The quadrate has a thickened posterior edge and dorsally articulates with the pterygoid arch. The pterygoid arch as far as can be judged consisted of two bones. Posteriorly the metapterygoid extends upwards to just below the parasphenoid and anteriorly the ectopterygoid forms a concave arch from the anterior edge of the quadrate to the vomer.

Sensory canal system. The sensory canal system of the head can quite easily be traced by the application of turpentine to the various bones. The supraorbital canal commences in the parietal and passes forward into the frontal. The bone preservation in that area is poor, and the canal can only be followed for a short distance. However, a further portion of the supraorbital canal can be traced in the postero-dorsal corner of the mesethmoid. Traces of the preopercular canal were found near the anterior border of that bone, and further evidence of it can be seen in the small separate preopercular plate above.

The infraorbital canal is continuous with the cephalic division of the main lateral line, and curves down through the dermopterotic. Its further passage is again obscured by the poor state of preservation in that area. The cephalic division of the main lateral line passes upwards on to the ventro-posterior margin of the parietal, where it gives off a well developed supratemporal commissure. The presence of this cross commissure on the hind margin of the parietal suggests that the parietal represents two bones, the parietal and the extrascapular. Posterior to the supratemporal commissure, the main lateral line turns downwards into the antero-dorsal corner of the supracleithrum passing diagonally backwards through this bone and then out on to the body scales as the main lateral line. The dorsal lateral line is a narrower canal, situated more superficially. It begins in the centre of the dorsal portion of the supracleithrum where it communicates with the main lateral line. It passes upwards and backwards to the dorsal edge of the supracleithrum, and then continues into the body scales, running along parallel with the dorsal margin of the body. It can be traced back almost to the dorsal fin.

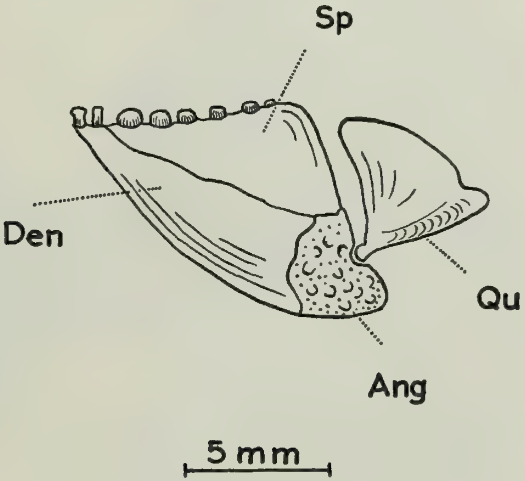

FIG. 52. *Eomesodon liassicus* (Egerton). Lower jaw and quadrate. From B.M.N.H. P 1336.

The main lateral line is well developed and its structure can be seen on B.M.N.H. P 5127. The canal appears to open to the surface between each scale, there being a distinct gap between the end of the canal on one scale and the recommencement of it on the succeeding scale. Anteriorly on each scale there is a fine ventral tubule which runs forwards and ends blindly (Text-fig. 53). The dorsal lateral line opens outwards by a small circular pit on the anterior border of each scale through which it passes.

Appendicular skeleton. The dermal bones of the shoulder girdle consist of a supracleithrum, a cleithrum and probably a postcleithrum. The anterior edge of the supracleithrum lies under the parietal and the dermopterotic. Between it and the cleithrum is another plate which could be an enlarged scale, but which is more probably the postcleithrum. The cleithrum itself is vertically elongated, tapering above and with a spatulate expansion beneath the opercular apparatus. The endoskeletal portion of the pectoral girdle has not been observed, and it was possibly only slightly ossified. The pectoral fin is attached just above the inferior expansion of the cleithrum. There is a single series of radials, six in number, all of which are somewhat expanded posteriorly. The lepidotrichia number about fifteen and are stout and segmented transversely. They dichotomize distally, but no fulcra have been observed along the anterior margin of the pectoral fin.

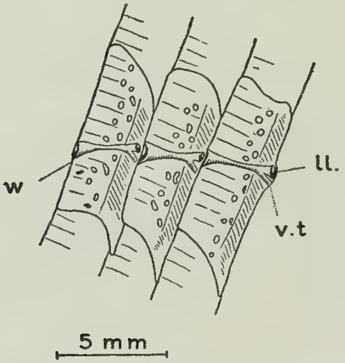

FIG. 53. *Eomesodon liassicus* (Egerton). Part of the squamation with a portion of the main lateral line. From B.M.N.H. P 5127.

The pelvic fins are not preserved on any of the specimens.

Unpaired fins. The lepidotrichia of the dorsal and anal fins are equal in number to their supports, which are more numerous than the neural spines in that region (Text-fig. 54). The number of lepidotrichia in the dorsal fin is about twenty-four, and these articulate with the rounded, expanded ends of the radials. The lepidotrichia bifurcate distally and are transversely segmented along their whole length. There are no traces of fulcra on either the dorsal or anal fins.

The anal fin is smaller than the dorsal with approximately fifteen lepidotrichia. Although these dichotomize distally, the transverse segmentation does not commence until the dichotomy begins.

The caudal fin has between eighteen and twenty lepidotrichia and its posterior margin is convex.

Axial skeleton. The notochord is persistent and the neural and haemal arches are well ossified. The neural and haemal spines of the vertebrae do not reach the dorsal border of the body, there being a set of radials interposed between the ends of the spines and the base of the fins. Neither the haemals nor the neurals bear laminar expansions in the caudal region. However, except near the tail the neural spines beneath the dorsal fin are double, each having a short slightly curved rod arising from the anterior portion of the neural arch, followed by the long backwardly directed neural spine proper.

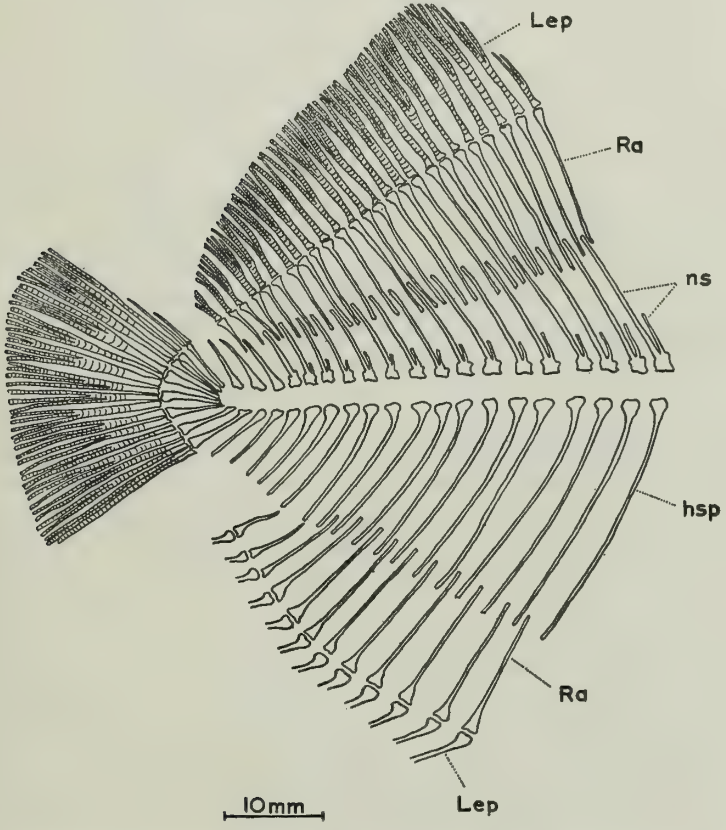

FIG. 54. *Eomesodon liassicus* (Egerton). Restoration of the endoskeleton of the trunk.

Squamation. The squamation is complete over the whole of the trunk in advance of the median fins. The scales are largest in the nuchal region and are ornamented with coarse tubercles, somewhat finer than those on the parietals and frontals.

The dorsal ridge scales are much deepened and modified ; the shape of the foremost ridge scales in the Worcester specimen being very different from that of the holotype. These dorsal ridge scales have the normal, median row of hooked denticles (4–6), those in front of the dorsal eminence being inclined backwards, those behind inclined forwards. The ventral ridge scales have no hooked or recurved denticles, but are more pointed just in front of the anal fin, somewhat resembling fulcral scales. Woodward (1918 : 56) gives the number of scales in a transverse series in the deepest part of the trunk as eight above the lateral line and ten below it. The majority of the scales are small, not much deepened and bear fewer tubercles than those in the nuchal region.

Order COELACANTHIFORMES

Family Coelacanthidae

Diagnosis. See Woodward, 1891 : 394.

Genus *HOLOPHAGUS* Egerton, 1861

1834 *Undina* Münster, p. 539 (nomen nudum)
1842 *Coelacanthus* Münster, p. 57 (in part).

Diagnosis. Trunk robust, dorsal fins well developed, supplementary caudal fin prominent. All the lepidotrichia are broad and stout, often expanded, and closely articulated in the distal portion. Small denticles are present on the preaxial rays of both the caudal and the first dorsal fins. External skull bones ornamented with tubercles and ridges of enamel. Plates of pelvic girdle distinctive (see Text-fig. 58). Basal plates of anal and second dorsal fins deeply bifurcated. Basal plate of first dorsal fin triangular. Dentition : teeth absent on jaw margins ; a few hollow conical teeth on the vomers and premaxillae.

Type species. *Holophagus striolaris* (Münster).

Remarks. The genus *Holophagus* has previously been known as *Undina* and attributed to Münster (1834 : 539). However, as used by Münster it is a *nomen nudum* and as in the same year it was used by Gould (1834, pl. 383) in describing a genus of birds, it is no longer valid for use in fish nomenclature. The first valid generic name was that used by Egerton (1861) when he described *Holophagus gulo*.

Two species, *Holophagus gulo* and *Holophagus barroviensis*, have been recorded from the Lower Lias of this country. The descriptions of both are inadequate by modern standards. The species *H.* (?) *barroviensis* according to Woodward (1891 : 413) " is imperfectly definable ", and that material which has been assigned to this species is, in my estimation, for the most part of doubtful affinities. As a consequence, the only certain species of Coelacanth recorded from the Lower Lias of this country is *Holophagus gulo*, and it is to the description of this species which I shall mainly confine my remarks.

Holophagus gulo Egerton

(Pl. 42 ; Text-figs. 55–58)

1861. *Holophagus gulo* Egerton, p. 19.
1866. *Holophagus gulo* Egerton : Huxley, p. 26, pl. 6.
1868. *Holophagus gulo* Egerton : Egerton, p. 502.
1872. *Holophagus gulo* Egerton : Huxley, p. 36, pl. 10.
1891. *Undina gulo* (Egerton) Woodward, p. 411, fig. 53.
1941. *Undina gulo* (Egerton) : Schaeffer, fig. 9*f*.

DIAGNOSIS. A *Holophagus* of large size, attaining a length of some 70 cm. Length of head about a quarter of the total length of the fish. Dorsal fins well developed.

HOLOTYPE. Fish, wanting head ; Geological Survey Museum, No. 28832 from the Lower Lias, Lyme Regis.

MATERIAL. Specimens in the B.M.N.H.

DESCRIPTION. *The skull.* There is only one specimen in the B.M.N.H. (P 2022*a*) showing the roofing bones in dorsal aspect, but their general shape can be made out from laterally crushed skulls (Text-fig. 55). The parieto-dermopterotics extend back on to the opercular and the postero-lateral corners are produced. The parieto-dermopterotics are separated from the frontals by a distinct suture, and in life these two bones must have connected by ligaments, thereby giving a movable joint as in other Coelacanths.

The frontals appear to form part of a continuous sheet until they meet the antorbital and the premaxillae. On one or two specimens there are doubtful cracks on the frontals anteriorly which may have been sutures, and in which case would have denoted the presence of the nasals. However, the sheet appears continuous up to the premaxillae and antorbitals, and there is no clear demarcation to denote the presence of separate nasals.

From the lateral borders of the lower surfaces of this sheet a series of bones surround the orbits. These are the supraorbitals (parafrontals) of which there are five, and the most anterior articulates with the antorbital in front and the postorbito-infraorbital bar beneath. The antorbital itself is a large bone with a branch of the sensory canal running through it. From its position and extent it probably represents the fusion of two ossifications, the antorbital and the postrostral. Beneath the antorbital is a characteristically-shaped bone noted by Watson (1921 : 330). It abuts on to the premaxilla anteriorly and the postorbito-infraorbital posteriorly. It is hollowed out beneath, and produced downwards at its anterior extremity. Watson (1921 : 330) has observed a similar bone in *Macropoma mantelli* Agassiz, and has suggested that these forward processes " perhaps separated the two nasal apertures ". However, by analogy with other previously described Coelacanths, and from the course taken by the sensory canal through this bone, I believe it to be correctly termed the rostral. Anterior to the rostral the premaxilla can be seen on specimen B.M.N.H. P 2022. The premaxillae are not fused as in *Macropoma*, but are separate and bear several large teeth (3–4).

The postorbito-infraorbital (lacrymo-jugal) is a complete bar beneath the orbit similar in shape to that in *Holophagus acutidens*. Anteriorly it articulates with the supraorbital and the antorbital.

The arrangement of the postorbitals and other cheek plates is somewhat different from that figured by Reis (1892*a*, fig. 1) for *Holophagus acutidens*, and also different from that figured by Woodward (1891, fig. 53) for *Holophagus gulo* itself. Fitting neatly beneath the posterior corner of the postorbito-infraorbital and covering the quadrate is a triangular-shaped bone, tapered anteriorly. This is homologous to the preoperculoquadratojugal of Stensiö (1937 : 12), and the preopercular of Moy-Thomas (1937 : 387). Above this bone and articulating with both it and the postorbito-infraorbital is a somewhat larger bone, the preoperculo-postorbital. Between the preoperculo-postorbital and the parieto-dermopterotic is a postorbital bone, smaller than the other two cheek plates, and articulating with the first supraorbital.

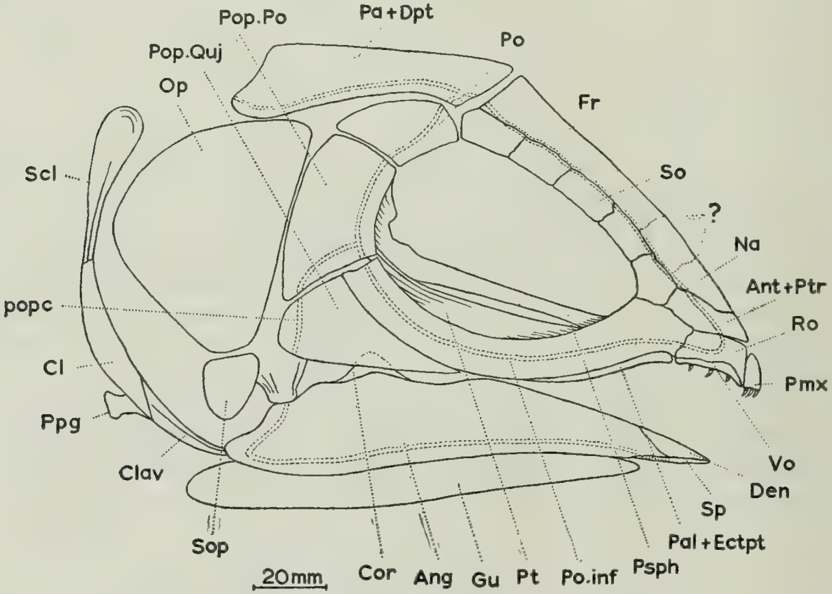

FIG. 55. *Holophagus gulo* Egerton. Reconstruction of the skull and pectoral girdle.

Behind the cheek plates is a large, roughly triangular-shaped opercular, well shown in B.M.N.H. P 3344. Beneath the opercular are traces of another small bone, presumably equivalent to the suboperculum of Reis (1892*a*, fig. 1). There is no evidence of a sclerotic ring, although this is present in the closely related *Holophagus acutidens*.

Lower jaw. In medial view the major portion of the lower jaw can be seen to consist of one bone, the angular (Text-fig. 56). This bone is continuous near its posterior end and no demarcation into a surangular can be found. Anteriorly it abuts on to the splenial and the dentary. These two bones are of approximately the same size, but are both much smaller than in other Coelacanths, particularly *Holophagus acutidens*. The position of the prearticular can be seen from Text-fig. 56. The coronoid appears to be much nearer the posterior end of the jaw than in other species of *Holophagus* being quite close to the articulatory facet. Between the rami of the jaws is a pair of delicately ornamented gular plates.

Neurocranium. The neurocranium can be seen in B.M.N.H. P 2022*a*, which shows the posterior portion of a dorso-ventrally flattened skull. In this specimen it is possible to recognize the basioccipital, prootic and basisphenoid in dorsal aspect (Text-fig. 57). The basioccipital forms a deep concave sheet, which projects behind the skull. It appears very similar to that figured by Aldinger (1930, fig. 6) for *Holophagus acutidens*. The prootic, which is continuous with the basioccipital, is a much smaller ossification and forms the main portion of the lateral walls of the neurocranium. Between the two prootics lies a large basisphenoid (this bone can also be recognized in B.M.N.H. P 2022). It is a stout ossification compared with the other bones, and its outer surface is convex, as though it were an articulating surface rather reminiscent of mammalian occipital condyles. The two foramina recognizable in the basisphenoid posteriorly transmitted the sixth nerve.

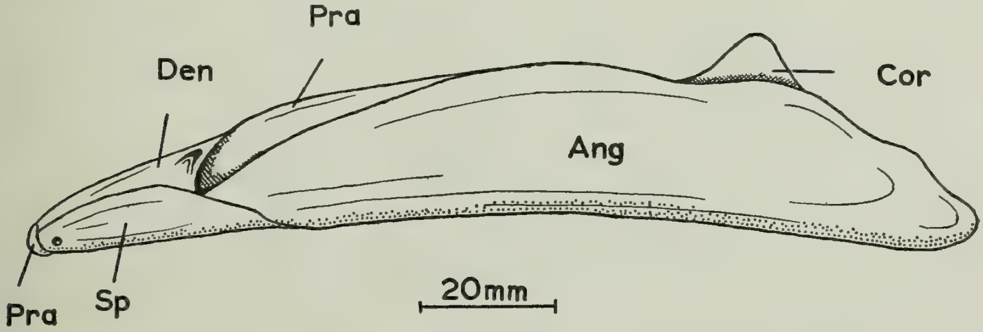

FIG. 56. *Holophagus gulo* Egerton. Restoration of lower jaw, based mainly on specimens B.M.N.H. P 2022 and P 3344.

The parasphenoid as it leaves the basisphenoid is comparatively narrow (B.M.N.H. P 2022), but as it runs forwards it becomes more spatulate. The neurocranial structure is generally very similar to that described for *H. acutidens* by Aldinger (1930 : 24) and also very similar to that described for *Macropoma mantelli* by Watson (1921, fig. 1).

Palate. On the articulated specimens little could be made out of the palatoquadrate apparatus. However, specimen B.M.N.H. P 9842 from the Great Oolite, Kingsthorpe, Northampton, consists of an isolated right pterygo-quadrate (Pl. 42). From its size it can probably be correctly assigned to the species *Holophagus gulo*, and as such will be described.

The major portion of the palate is formed by an enlarged pterygoid ; this bone (Pl. 42) is rather unusual in shape and quite different from that of any Coelacanth so far described. It is triradiate anteriorly, with a strong median ridge running well forward. Its dorsal edge is distinctly concave and also extends well forward, in contrast to the more upright nature of the pterygoid seen in other Coelacanths (*Axelia, Wimania, Macropoma, Nesides* etc.). Dorsally it articulated with the metapterygoid. On its inner surface the pterygoid bears small tubercular teeth, but these are restricted to the lower edge and upper rim. On the outer surface the quadrate is completely fused with the pterygoid, in the postero-ventral corner, but the quadrate can be clearly recognized from its distinctive ossification, with radiating lines running forwards (Pl. 42).

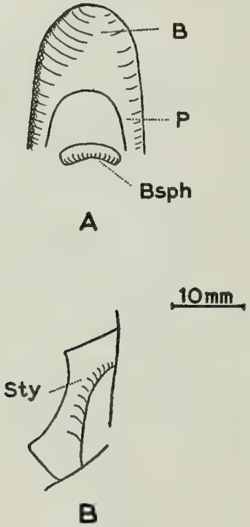

Fig. 57. *Holophagus gulo* Egerton. A, dorsal view of neurocranium. From B.M.N.H. P 2022*a* ; B, stylohyal, from B.M.N.H. P 3344.

A pterygo-quadrate from an obviously distinct species is shown in Pl. 43. It is B.M.N.H. P 959 from the Stonesfield Slate, near Oxford. It is much more elongated posteriorly, and its lowermost edge, which abuts on to the ectopterygoid and autopalatine, is very much shortened.

The palatine, ectopterygoid and vomers can only be seen on the majority of the specimens in lateral view. They project down beneath the postorbito-infraorbital bar, and run forwards to the maxillae. The ectopterygoid is the most posterior and is long and delicate, bearing very small teeth. This bone is often termed the maxilla, but Watson (1921, fig. 1) recognized it as a true ectopterygoid. In front of this bone are two similar ossifications, both bearing minute teeth. The first is the palatine and the most anterior the prevomer (pre-ethmoid of Stensiö, 1921, fig. 19).

Behind the opercular in B.M.N.H. P 3344 is a stoutish bone, almost hour-glass in shape and nearly vertical in position. This bone is the stylohyal (Text-fig. 57), but no other remains of the branchial arches could be found.

Sensory canal system. The main cephalic division of the sensory canal runs round the edge of the parieto-dermopterotic and no supratemporal commissure is recognizable in the posterior region, hence this compound sheet of bone does not contain the extrascapular. Just before it leaves the parieto-dermopterotic and passes into the frontal, the sensory canal branches to give the infraorbital canal. The infraorbital canal passes downwards through the postorbital and through the anterior edge of the preoperculo-postorbital. In the latter bone it gives off the preopercular sensory canal posteriorly. The infraorbital canal continues on through the length of the postorbito-infraorbital and into the rostral. Here it turns upwards and through the antorbital and into the lateral ventral edge of the nasal as the supraorbital canal. The supraorbital canal runs back up through the length of the frontal, its course being marked by pits both in the lateral edge of the frontal and in the dorsal edges of the supraorbitals. It finally fuses with the main cephalic division in the antero-lateral corner of the parieto-dermopterotic. The preopercular canal runs diagonally down through the preopercular-postorbital. The latter canal continues on down through the posterior edge of the preoperculo-quadrato-jugal bone.

The mandibular canal is marked by a double series of pits, and enters the lower jaw dorsally near the articulation. At first the canal runs backwards and downwards, but it then curves sharply round to run the length of the angular bone, and ends up in the splenial just short of the prearticular.

Appendicular skeleton. The pectoral girdle in both *Holophagus* and *Macropoma* has a backwardly directed portion of the endoskeleton attached to it. This bone shows no sutures in *Holophagus gulo* and probably represents the fusion of a scapula and coracoid. It occurs just posterior to where the cleithrum and clavicle articulate, and to it the skeleton of the pectoral fin must have been joined.

The girdle itself is complete and seen in B.M.N.H. P 2022 and P 3344. The supracleithrum is comparatively thin and rather spatulate in outline, with several strengthening ridges running down it. The cleithrum is of similar dimensions, and near its ventral extremity it has this short posteriorly-directed projection mentioned above. The clavicle runs on down from the cleithrum, and like the supracleithrum it has strengthening ridges along its length.

The pectoral fin has from fifteen to twenty fin-rays with a comparatively narrow insertion.

The pelvic plates of *Holophagus minuta* (Reis) (this is probably founded on young specimens of *Holophagus striolaris* (Münster)) and *Holophagus acutidens* have been well figured and it only remains to figure those of *Holophagus gulo* for comparison. The figure of Woodward (1891, fig. 53) is very misleading, and I have never seen a pelvic plate of *Holophagus gulo* looking anything like his drawing.

Anteriorly each plate is much expanded and sheet-like, with a strengthening ridge running down both of the lateral edges (Text-fig. 58). Although of much the same general shape, it differs in detail both from that found in *H. minuta* and in *H. acutidens*.

The pelvic fin shows seventeen to eighteen fin rays, but the insertion is larger than that of the pectoral fin.

Unpaired fins. The basal plate of the first dorsal fin is of typical Coelacanth form, triangular in shape with its apex directed forwards.

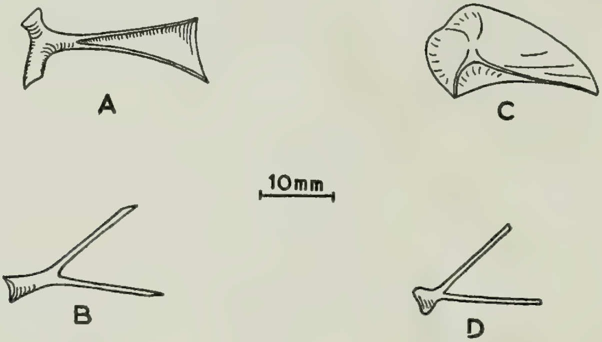

Fig. 58. *Holophagus gulo* Egerton. Plates supporting fins. A, pelvic plate ; B, basal plate of anal fin, right side ; C, basal plate of first dorsal fin, right side ; D, basal plate of second dorsal fin, right side.

The fin itself is well developed with ten stout rays visible. The basal plate of the second dorsal fin is a bifurcated structure with the open part of the V directed forwards. Its fin has from fifteen to eighteen rays, with a broader insertion than that of the first dorsal.

Again the anal fin has a deeply bifurcated plate similar to that of the second dorsal fin. Schaeffer (1941 : 12) suggests that this type must have arisen by the development of an antero-ventral process from the posterior expanded division. There is no evidence of a median keel projecting ventrally as figured by Woodward (1891, fig. 53).

The fin is more delicate than the others and shows from between seventeen and eighteen fin rays, rather more slender and closely articulated distally.

Axial skeleton. The axial skeleton is as figured by Woodward (1891, fig. 53).

III. DISCUSSION

As an introduction to the discussion, a Table is given below listing the differences between the Palaeoniscoid condition and the condition found in the Holostei.

Palaeoniscoid condition	Holostean condition
1. Maxilla fixed, in articulation with the preopercular and postorbital bones.	1. Maxilla and preopercular reduced and completely separated. The preopercular is quite narrow dorsally while the maxilla only articulates with the snout.
2. Interopercular absent.	2. Interopercular present.
3. Suspensorium normally oblique.	3. Suspensorium vertical or slightly directed forward.
4. Coronoid process absent.	4. Coronoid process present.
5. Antorbital absent, nasals border orbit.	5. Antorbital present, nasals generally excluded from orbit.
6. Postrostral bone separates the nasals.	6. Postrostral bone only present in the early Semionotidae.
7. Pectoral and pelvic lepidotrichia usually completely segmented transversely.	7. Pectoral and pelvic lepidotrichia only distally transversely segmented.
8. Dorsal and anal fin-rays completely segmented transversely and are more numerous than the endoskeletal supports.	8. Dorsal and anal fin-rays partly segmented transversely and equalling the endoskeletal supports in number.
9. Clavicle present.	9. Clavicle absent.
10. Neurocranium completely ossified, individual bones fused and sutures not apparent.	10. Neurocranium either completely ossified or partially cartilaginous, in both cases individual bones clearly visible.
11. Tail unreduced and heterocercal.	11. Scaly lobe usually much reduced and tail hemiheterocercal or rarely homocercal.
12. Scales consists of three layers; a lower layer of lamellated bone, and intermediate layer of dentine (cosmine), the whole capped by a layer of enamel. Canals of Williamson and dential tubules numerous.	12. Scales consisting of a lower layer of lamellated bone and an upper layer of enamel. Dentine layer and dential tubules normally missing. (*Lepidotes minor* still has dentine, Gross, 1935 : 48.) Canals of Williamson undergoing reduction.

The Origin and Affinities of the Holostei

The earliest Palaeoniscoid to show any development towards the Holostean condition is *Canobius*. It had already acquired an upright suspensorium by the Lower Carboniferous. Many later forms have also developed this vertical suspensorium quite independently of one another. Examples outside the Holostei proper include *Haplolepis*, *Pyritocephalus*, *Aeduella*, *Lepidopterus*, *Platysomus*, *Bobasatrania*, *Meridensia*, *Platysiagum* and all Parasemionotidae.

Other typically Holostean characters can also be found amongst the pre-Triassic fish fauna. *Phanerorhynchus* (Gill, 1923*a* : 465) shows a reduction in the number of fin-rays, whilst the general appearance of the trunk is distinctly Holostean. *Phanerosteon* (Fritsch, 1893) has the same number of radials as fin-rays and ossified vertebral centra resembling hollow cylinders, and *Pyritocephalus* and *Haplolepis* (Westoll, 1944) both show several Holostean characters besides an upright suspensorium. In most Palaeoniscoids and many Holosteans the supraorbital sensory canal remains separate from the infraorbital, but in the earliest Holostean *Acentrophorus* (see Text-fig. 69) the supraorbital canal fuses with the main cephalic division where it turns down as the infraorbital canal. This change-over from the first to the second type, clearly shown in the development of *Amia*, (Allis, 1889) has been independently achieved at least three times (Brough, 1936). Watson (1925 : 867) has shown it in the Palaeoniscoid *Oxygnathus ornatus* and Wade (1935 : 21, fig. 5) in the Catopterid *Brookvalia*.

The independent development of Holostean characters has already been emphasized within the group Subholostei by Brough (1936 : 388). Westoll (1937*b* ; 1944 : 98) working on *Aeduella* and the Haplolepids supports this view and states that it is reasonable to suppose that Holostean characters have been acquired independently in different forms. Again Stensiö (1932 : 295) stresses the resemblance between the Pholidopleuridae (Subholostei) and the later Pholidophoridae (Holostei). Further, Westoll (1944 : 67) points out the similarities between *Haplolepis ovoidea* and the generalized Holostean. He shows that the maxilla of *Haplolepis ovoidea* has lost all traces of its cheek expansion and that by very little modification it could be freed from the preopercular resulting in a thoroughly Holostean condition. The Haplolepids show beautifully that such developments can occur in closely allied fishes, and indicate the scale of changes necessary for the production of Holostean characters (Text-fig. 59).

The most significant difference between the Palaeoniscoids on one hand and the Holosteans on the other is this question of jaw suspensions. It is difficult to see why some of the Palaeoniscoids with their wide gape and much inclined suspensorium should change towards a more vertical jaw suspension. At first sight the Palaeoniscoid jaw appears to be perfectly adequate, and furnished with a continuous series of powerful teeth, there seems little reason for alteration. Regan (1923 : 460) and Watson (1925 : 868) both agree that the changes in the nature of the suspensorium took place in association with a change in habit of the fishes concerned, and Westoll (1937*b* : 576) suggests its correlation specifically with changes in feeding habits. However, once the upright suspensorium had been acquired, then innumerable subsequent alterations to a variety of other skull bones became possible. For example, the cheek bones were no longer needed to provide a rigid side wall to the skull in order to resist the stresses and strains of muscle action, but were free to develop independently. Westoll (1944, fig. 44) has already shown what remarkably different patterns of cheek bones can be produced in the Haplolepidae once an upright suspensorium had been acquired. Other changes intimately linked with the acquisition of an upright suspensorium included a change in position of the maxilla. This moved forwards and became free from the preopercular, and simultaneously other changes occurred in the region of the snout. The projecting rostrum is reduced and finally lost (Parasemionotidae), whilst other changes occurred in the palate. In the palate the upper margin of the pterygoid became separated from the maxilla, and once the quadrate had secured sufficient support, by connection between the metapterygoid, preopercular and hyomandibular, then the freeing of the maxilla became possible. In the Palaeoniscoid condition, the *musculus adductor mandibulae* was more or less horizontal, lying within the palatoquadrate-maxillary apparatus and lower jaw, and having its origin on the palatoquadrate. Later, with this change in support of the quadrate, the *musculus adductor mandibulae* shifted its origin to a much more backward and vertical position (on to the anterior rim of the preopercular). Finally, the shortening of the mouth is accompanied by the formation of an interopercular, probably from the first branchiostegal ray (Piveteau, 1934 : 160). Stensiö (1932 : 98) put forward the suggestion that there was a definite functional correlation between the freeing of the maxilla and the modification of the dermal bones in the snout area, while Westoll (1944, fig. 47) has shown diagrammatically how it is possible to derive a Holostean type of cheek, snout and palate from a Palaeoniscoid one simply by

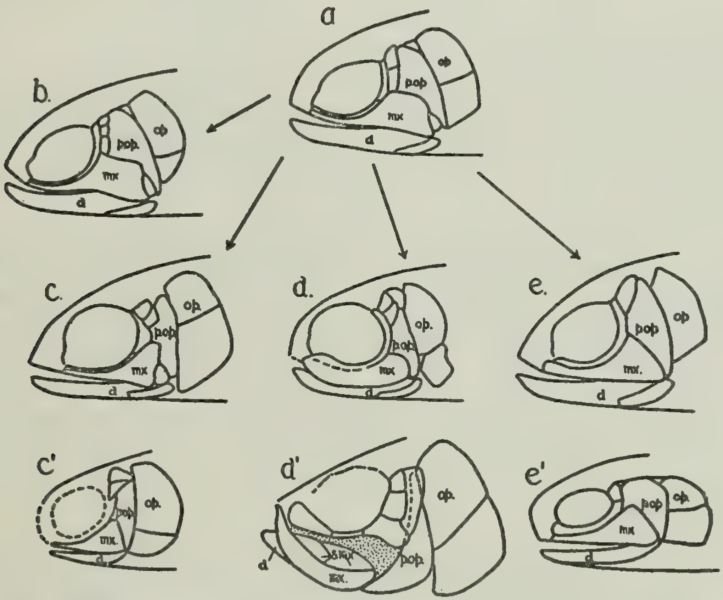

FIG. 59. Derivation of different Haplolepid cheek patterns, with examples of convergent structure in later Actinopterygians from Westoll (1944). a, cheek of X ; b, *Pyritocephalus sculptus* Fritsch ; c, *Haplolepis* (*Parahaplolepis*) *tuberculata* (Newberry) ; *d*, *H.* (*H.*) *ovoidea* (Newberry) ; *e*, *H.* (*H.*) *corrugata* (Newberry) ; c^1, *Peltopleurus lissocephalus* Brough (after Brough) ; d^1, *Leptolepis coryphaenoides* Bronn (modified after Rayner) ; e^1, *Perleidus madagascariensis* Piveteau (after Piveteau).

alterations in the angle of the suspensorium and the reduction of the ventral parts of the snout.

The reasons and advantages of these changes are several and all closely interrelated. Undoubtedly the most important advance from the Palaeoniscoid condition was this freeing of the maxilla coupled with the straightening of the suspensorium. Once this had occurred then the swinging forward of the lower jaw became possible and with it a much more efficient means of food capture. On opening, the lower jaw could now protrude forwards in front of the upper, and by hinging of the remainder of the cheek apparatus, the sucking action so characteristic of the Teleosts was evolved, and prey instead of being actively hunted down could now be " gulped " into the mouth from a short distance. The freed double-hinged maxilla forming the outer and more backward boundary to the mouth thereby prevented the prey escaping, whilst the formation of a toothed premaxilla (from a fragmentation of the tooth-bearing rostral elements) was also an asset in this respect.

One of the main reasons for bringing about these changes can be related to similar occurrences in the tetrapods. Within the bony sheath formed by the palato-quadrate-maxillary apparatus there was little or no room for the adductor mandibulae muscle to " belly " out, thus the rigid walls of the cheek broke up to allow for this increased expansion.

Once this break up of the rigid cheek walls had occurred, then with only a moderate change in the insertion of the adductor mandibulae muscle, a much more powerful jaw action would be acquired (coupled with the development of a coronoid process on the lower jaw at about the same time). Thus the early Holosteans could now not only bite harder but were free to develop powerful crushing dentitions. Within the Holostei a powerful crushing dentition is met with in the Pycnodonts and Lepidotids, whilst the Palaeoniscid ancestors to the Pycnodonts, the Amphicentrids, have a similar but less robust dentition. These forms occupied the evolutionary niche vacated by the Dipnoi, and were responsible for the rapid decline of the Dipnoans in the early Mesozoic.

The question of the origin of the Holostei can be examined. Romer (1945 : 580) in his classification retains the super-order Holostei and within it the five orders : Amioidea, Semionotoidea, Pholidophoroidea, Aspidorhynchoidea and Pycnodontoidea. For the sake of convenience I shall adhere in this discussion to the broad lines of his classification, giving superfamily designation where he has used orders.

AMIOIDEA

The Holostei have been regarded by many authorities (Regan, 1904, 1923, 1929 ; Gregory, 1923, 1933) to be a uniform group of closely-related fishes, monophyletic in origin. Stensiö (1932 : 296) first put forward the idea that perhaps the Holostei were really a polyphyletic group, and this view has been supported by Brough (1939), Westoll (1944), Piveteau (1941) and Lehman (1952). Rayner (1941, 1948) considers the origin of the Holostei an open question, but appears to favour the monophyletic view. Schaeffer & Dunkle (1950 : 25) also believe the evidence to be inconclusive, but point out that the Semionotids, Amioids, and Pholidophoroids have essentially the same roof pattern, and on this and other evidence they suggest that Semionotids and Amioids had a common ancestral stock in the Permian, whilst the Pholidophoroids may have evolved from that same stock, possibly the Parasemionotids, at a later time.

Until the description of the Lower Triassic family the Parasemionotidae (Text-figs. 67, 68) by Stensiö (1932) and Piveteau (1934), all the Holostei were believed to have arisen from the same unknown Palaeoniscoid stock.

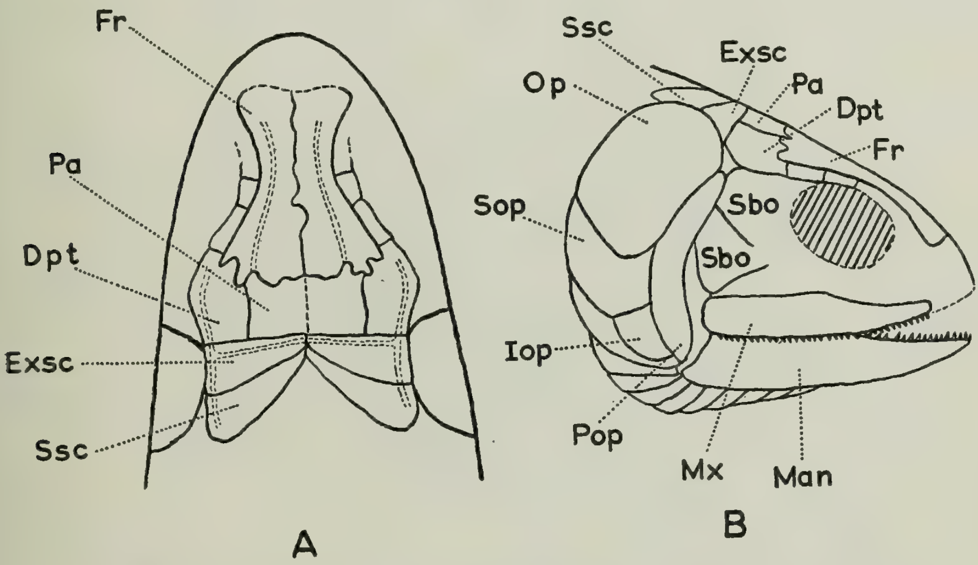

FIG. 60. *Eoeugnathus megalepis* Brough. Reconstruction of skull in A, dorsal view; B, lateral view. After Brough (1939).

The Parasemionotidae resemble the later Furidae (Text-fig. 60) in many details of skull structure. Brough (1939 : 91) first emphasized the unmistakable similarities between these two families, pointing out in both the identical small parietals and large dermopterotics, the similar relationships in size and shape of the extrascapular and suprascapular, the proportions of the frontals bordered in each by a row of supraorbitals, the similar dermosphenotics and the presence of large paired nasals. Both families have interoperculars and an almost identical jaw structure. In contrast to the Furidae the Parasemionotidae lack suborbitals and have a relatively unreduced preopercular.

Lehman (1952) has shown that in some Parasemionotids from the basal Trias of Madagascar suborbitals are being formed by anamestic fragmentation of the anterior part of the preopercular (see p. 340 for further details). Therefore he concludes that the Parasemionotids are probably ancestral to the Furids.

Since the Parasemionotidae arose from the Palaeoniscoids some time during the Permian (or even earlier), the Semionotidae must have arisen from the Palaeoniscoids independently of the Furidae for the following reasons :

(*a*) A typical Semionotid (*Acentrophorus*) exists in the Upper Permian.

(*b*) Early Furids resemble Semionotids less than later ones, and many of the resemblances between the Furidae and Semionotidae are due to convergence.

At this stage in the discussion it would be as well to look into the origin of the Holostean suborbitals (postorbitals). The first suggestion comes from Watson (1925 : 868) who states that the bone occurring in the Palaeoniscid *Coccocephalus wildi* between the anterior border of the preopercular and the infraorbital series may give some indication as to the possible source of the suborbital plates of the Lepidostei. Later (1928 : 58) he states that the series of three bones in *Elonichthys caudalis* and two in *Elonichthys serratus* (Text-fig. 75), which lie along the anterior edge of the preopercular (between it and the posterior infraorbitals) are the source for the suborbitals of the Holostei. Aldinger (1937 : 364) puts forward a different view. He considers that the Holostean suborbitals have arisen by a breaking up of the anterior expanded area of the Palaeoniscid-Subholostean preopercular. Further, he believes it to have occurred independently in several of the Palaeoniscids and Subholosteans. This is supported by the presence of supramaxillary and postmaxillary sensory lines on the preopercular of the Parasemionotidae while in some Holostei (*Lepidotes*, Westoll, 1957*a*, fig. 7), *Semionotus capensis* (Text-fig. 71) and

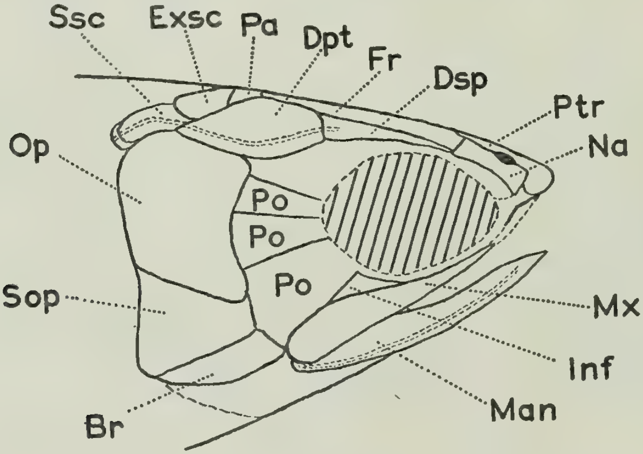

FIG. 61. *Ptycholepis curta* Egerton. Restoration of skull in lateral view. After Brough (1939).

Osteorachis macrocephalus (Text-fig. 24) they have become transferred to the suborbitals. Other evidence he cites includes the presence of a small bone beneath the preopercular in *Ospia* (Stensiö, 1932, fig. 84) and also three small bones above the preopercular in *Parasemionotus*. Aldinger links this breaking up of the preopercular with the acquisition of an upright suspensorium, but as Schaeffer & Dunkle (1950 : 19) point out, this theory does not explain the presence of suborbitals in forms like *Glaucolepis* (Nielsen, 1942, fig. 30) and *Palaeoniscus freieslebeni* (Aldinger 1937 : 102) which still retain an expanded preopercular, or in forms like *Canobius* (Moy-Thomas & Dyne, 1938 : 440) with an expanded preopercular and a vertical suspensorium.

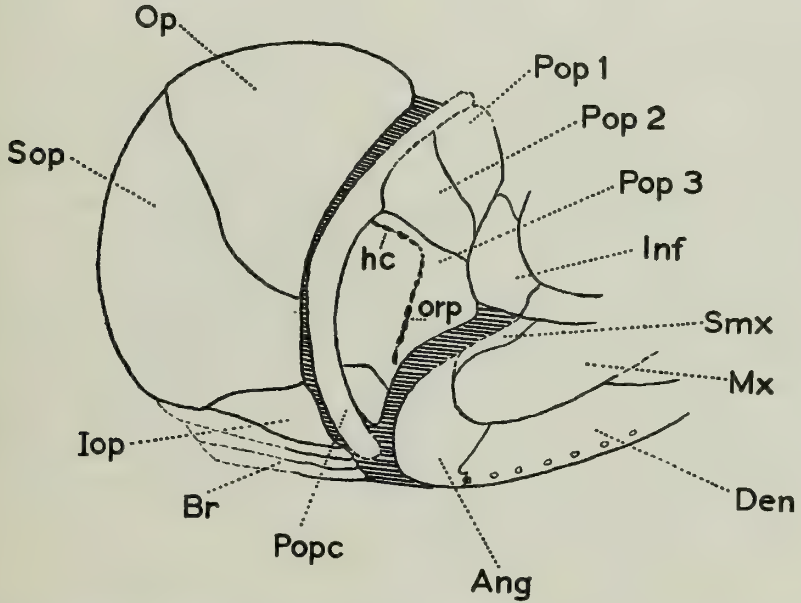

FIG. 62. *Thomasinotus divisus* Lehman. Fragmentation of the preopercular. From Lehman (1952).

Finally, Stensiö (1947 : 148) considers the suborbitals of the Palaeonisciformes and Subholostei to have been derived either from the anamestic components of the adjoining postorbital infraorbitals or from the anamestic anterior part of the preopercular, or from both sources. Thus he considers them not to be equivalent in the individual forms possessing them.

As to the origin of the Holostean suborbitals, Stensiö (1947 : 154) puts forward two theories. The first is that they arose by a subdivision of the anterior parts of the whole Palaeonisciform preopercular into independent minor plates. This is exactly comparable to the theory put forward by Aldinger (1937 : 363), and Stensiö bases it also on an interpretation of the three bones above the preopercular in *Parasemionotus* as being suborbitals derived from the anamestic components of the preopercular. His second theory is that the suborbitals of the Palaeoniscids and Subholostei have been directly inherited (Watson, 1925 : 868 ; 1928 : 58). For these suborbitals to acquire the Holostean condition, Stensiö (from an interpretation of Brough's, 1939 : 66, description of *Ptycholepis curta* ; Text-fig. 61) suggests that they underwent an excessive outgrowth backwards, over the anterior portion of the preopercular, which was consequently reduced. Then as the anterior portion of the preopercular was eliminated, the superficial sensory lines (supramaxillary and postmaxillary) carried thereon would have been forced to shift to the skin laterally to the suborbitals, and would thus become secondarily situated outside these bones. Schaeffer & Dunkle (1950 : 21) summing up the evidence, believe that the palaeontological data alone would favour Stensiö's second theory for the origin of Holostean suborbitals.

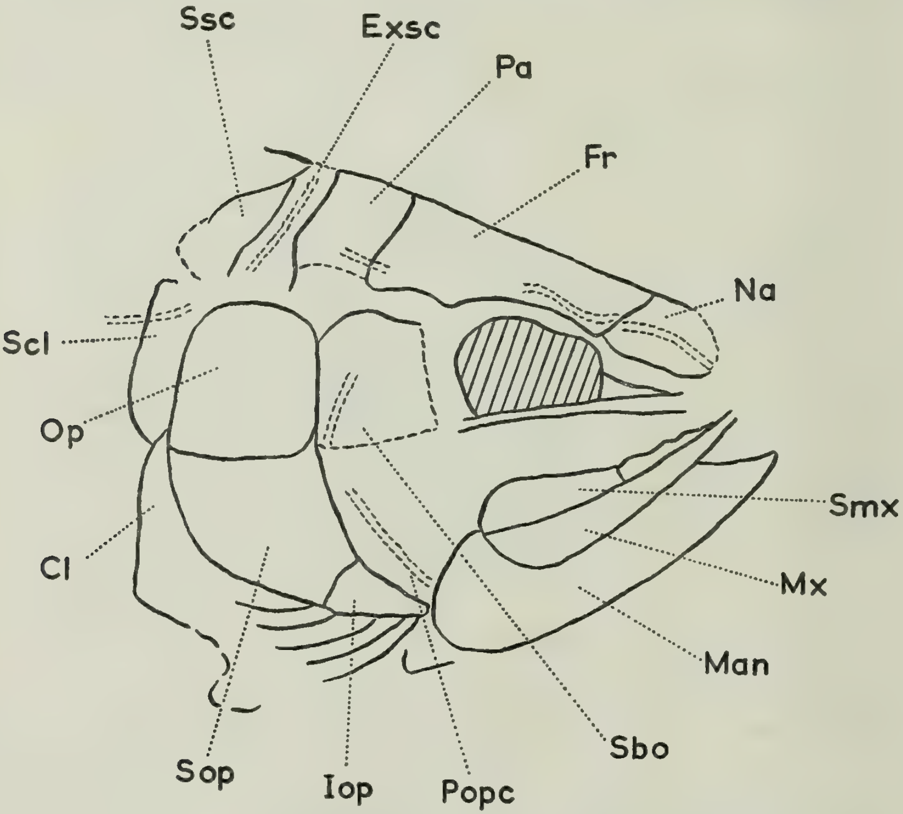

FIG. 63. *Promecosomina formosa* (Woodward). Skull in lateral view, after Wade (1941).

In 1952 Lehman described three new Parasemionotid genera from the basal

Trias of Madagascar. These were *Stensiönotus, Jacobulus* (Text-figs. 62, 67) and *Thomasinotus*. In his description Lehman shows that the preopercular in all three forms shows division into different plates and that the disintegration of the anterior portion of the preopercular as proposed by Aldinger (1937 : 363) and Stensiö (1947 : 154, 1st hypothesis) really took place. In fact there are true suborbitals present as Brough (1939 : 93) suspected. Having shown that fragmentation and reduction of the preopercular were taking place in the Parasemionotidae, Lehman proves beyond doubt that the Parasemionotid stock must have been ancestral to the Furidae and hence the entire Amioidea. Further he proves that in the Furid stock of Holosteans, the suborbital series arose by anamestic fragmentation of the preopercular.

Together with the three new forms, the basal Trias of Madagascar has yielded five genera belonging to the family Parasemionotidae : *Watsonulus, Parasemionotus, Stensionotus, Jacobulus* and *Thomasinotus*, and Lehman lays emphasis on the very rapid evolution which this family must have been undergoing in the early Trias. Other genera included in the family Parasemionotidae are the two forms from the basal Trias of Greenland, *Broughia* and *Ospia* described by Stensiö (1932). The reception of these last two genera in the Parasemionotidae has been justified by Stensiö's (1937) subsequent discovery of a true interopercular in some of the Ospiids. Lehman (1952 : 185) also called attention to the similarity between the Parasemionotidae and the Promecosominidae. From a study of Wade (1935, 1941) he suggested that since *Promecosomina* has a divided preopercular, both halves of which contain a portion of the preopercular canal (see Text-fig. 63), the dorsal division of this bone could not be a suborbital plate as Wade (1941, fig. 1) labelled it. Lehman therefore concluded that *Promecosomina* was a true Parasemionotid and that the family Promecosominidae must be abandoned, with which view Wade (1953 : 72) later agreed. In order to test the validity of his conclusion, I examined some samples of *Promecosomina*.

Genus ***PROMECOSOMINA*** Wade, 1935

DIAGNOSIS. See Wade, 1935 : 80 ; 1941 : 380.
TYPE SPECIES. *Promecosomina formosa* (Woodward).

Promecosomina formosa (Woodward)

(Text-figs. 63, 64)

1908. *Acentrophorus* sp. Woodward, p. 21.
1908. *Semionotus formosus* Woodward, p. 23, pl. 4, fig. 8.
1908. *Pholidophorus australis* Woodward, p. 26.
1935. *Promecosomina beaconensis* Wade, p. 80, pl. 8, figs, 3, 4 ; text-fig. 46.
1941. *Promecosomina formosa* (Woodward) Wade, p. 382, pl. 17 ; text-figs. 1–3.
1953. *Promecosomina* Wade, p. 72.

DIAGNOSIS. See Wade, 1935 : 80 ; 1941 : 382.
HOLOTYPE. Specimen in the Australian Museum, Sydney, F 38905, figured by Woodward, 1908, pl. 4, fig. 8, an imperfect fish lacking pectoral fins from the Hawkes-

bury Series at St. Peters, N. S. Wales, and counterpart in the B.M.N.H. P 18091.

MATERIAL. Specimens in the B.M.N.H.

DESCRIPTION. *The skull.* These specimens came from the Upper Trias (Hawkesbury) of St. Peters, N.S.W. A reasonably complete dorso-ventrally flattened skull roof can be seen on B.M.N.H. P 18072, in which the parietals, frontals, nasals, dermopterotics, extrascapulars and suprascapulars are all visible. The parietals are small, paired and nearly square in outline (Text-fig. 64). On either side are the elongated, narrow dermopterotics. The frontals, which are broad posteriorly, narrow between the orbits. Anteriorly the nasals abut on to the premaxillae as can be seen in B.M.N.H. P 18092, but the state of preservation is too poor to be able to discern teeth on the latter bone. Adjoining the hinder margin of the parietals is a pair of triangular extrascapulars. These meet on the mid-line in a short suture.

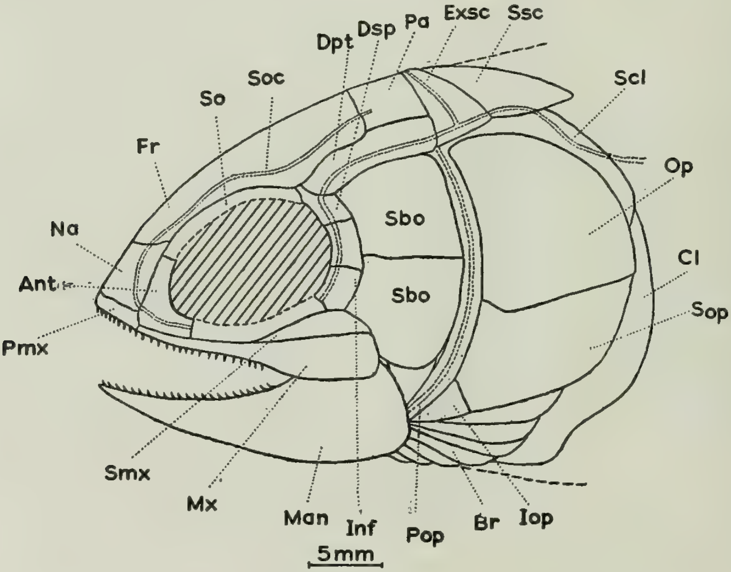

FIG. 64. *Promecosomina formosa* (Woodward). Reconstruction of skull in lateral view.

Behind the extrascapulars are the well-developed suprascapulars. These bones are also triangular and extend posteriorly well back over the anterior region of the trunk. In front of the opercular is a long preopercular curved gently forwards at its lower end. Throughout its length it is narrow and the preopercular canal runs through it, as can be seen on several of the B.M.N.H. specimens, as a calcite cast. Anterior to the preopercular is a pair of suborbital plates. These are both quadrangular in general shape, and the more dorsal member often completely overlaps the dorsal region of the preopercular. Specimens which show clearly both suborbital and preopercular plates are, B.M.N.H. P 18091, P 18092 and P 18093. Although Wade (1941 : 386) could find little evidence of a circumorbital series, a complete one did exist, as is shown by B.M.N.H. P 18091. With difficulty a small dermosphenotic, lying beneath the dermopterotic and anterior to the dorsal suborbital, can be made out on this specimen. Below it are two further members of the infraorbital series, limiting the orbit posteriorly. The exact number of these infraorbitals cannot be ascertained. The anterior region of the snout is well shown in B.M.N.H. P 18092. The antorbital is large and abuts on most of the posterior edge of the nasal, and ventrally meets the premaxilla and maxilla. There is evidence of a supraorbital series, but the number of individual bones cannot be ascertained. The sensory canal system of the head is as Wade (1941 : 387, fig. 1) described, except that the infraorbital sensory canal travels down through the dermosphenotic and round the infraorbital series into the antorbital, whence it appears to pass up into the nasal as the supraorbital canal. An adequate description of the remainder of the skull and body is given by Wade (1935, 1941).

It is clear that *Promecosomina*, with its well-developed suborbitals overlapping the preopercular, is more advanced than the earlier Parasemionotids. *Promecosomina* is a good freshwater Holostean and the family Promecosominidae must be retained for its inclusion. It resembles the Furidae in its fusiform trunk with an almost straight dorsal edge, in the slight forward inclination of the suspensorium and the accompanying moderate curvature of the preopercular, the long maxilla, well-developed supramaxilla and the interopercular which does not reach far forwards. Thus, like the Furidae, it was undoubtedly descended from the Parasemionotidae and can be correctly placed with the former in the Amioidea.

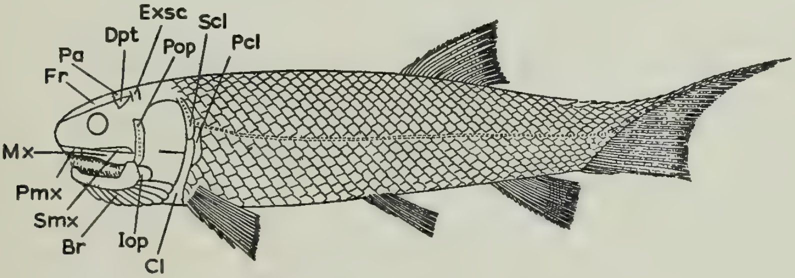

FIG. 65. *Tungusichthys acentrophoroides* Berg. From Berg (1941).

Fairly closely allied to the Parasemionotidae is the family Tungusichthyidae erected by Berg (1941 : 461) to include the solitary genus *Tungusichthys* (Text-fig. 65) from the Lower Trias of the Tunguska Coal Basin, Siberia. This family differs from the Parasemionotidae in possessing a narrow vertical preopercular (very similar to that found in the Furids) and in the shape of the frontals and maxillae. The caudal fin is almost homocercal and from the few known facts about the family there is much to be said for associating it with the Parasemionotidae in the superfamily Ospiiformoidea.

Thus the Parasemionotidae is a large group, whose origin is somewhat obscure. Brough (1939 : 94) suggested their derivation from a Palaeoniscoid such as *Pteronisculus*. This is impossible since *Pteronisculus* already has a suborbital series present (formed probably from a division of the infraorbitals). Again this rules out several other of the Palaeoniscoids with a more or less upright suspensorium and a suborbital series. Piveteau (1941 : 88) postulates a relationship between the Parasemionotidae and the Perleidids. It is possible that these two groups had a common ancestral stock in the Permian.

Returning to the Amioidea : the family Furidae forms the central group of the Mesozoic Holosteans, and bears close relationship to the later Amiidae (Brough, 1939 ; Rayner, 1941, 1948 ; Schaeffer & Dunkle, 1950). The group as a whole shows a rather conservative history, culminating in the more specialized Macrosemiids and Pachycormids. The evolutionary trends within the Macrosemiids have been discussed at length by Saint-Seine (1949 : 287). The Pachycormidae which Rayner (1941 : 229) finds too specialized to include with any other family and with which view Westoll (1944 : 85) agrees, have been shown by Lehman (1949 : 39) to have unmistakable Amioid resemblances, despite several pronounced specializations.

Observations on the neurocrania of *Caturus, Heterolepidotus* and *Osteorachis* by myself, bear out Lehman's (1949 : 39) conclusions. Rayner (1948 : 296) in her study of *Caturus*, from the available material was unable to decide whether or not there was an independent ossification in the posterior otic region (i.e. a Holostean opisthotic). However, I have been able to recognize in *Caturus chirotes* a separate ossification in that area. The ossification is interpreted by me as an opisthotic (Text-fig. 36). In *Osteorachis* the brain case is solidly constructed, and consequently sutures are difficult to recognize, but each ossification is distinct, with the bone fibres radiating in a regular fashion from the centre of the ossification. Thus it is again possible to distinguish a separate ossification, above the intercalar in the posterior otic region, and this bone must be an opisthotic (Text-fig. 26). The same bone also occurs in a similar position in *Heterolepidotus* (Text-fig. 29). In comparison, the neurocrania of *Pachycormus* (Rayner, 1948, figs. 18, 30) and *Hypsocormus* (Stensiö, 1935, fig. 6) both have an opisthotic present in the lateral wall. One other point of similarity between the neurocrania of the Pachycormidae and the Furidae is the absence of a supraoccipital. In conclusion, a comparison with the neurocrania of *Sinamia* (Stensiö, 1935, figs. 1, 2) and *Amia* must be made. In both these forms the opisthotic is missing. This is not considered to be of primary importance, but rather to be connected with a progressive lightening of the skull as a whole in *Sinamia* and *Amia*. Lastly, as Lehman (1949 : 40) indicates, in the general skull structure, shape of parasphenoid, the course of the arteries and the pharyngeal supports, *Pachycormus* seems closer to *Amia* than to any other of the Amioidea.

One remaining genus, placed by Piveteau (1941 : 78) in the Semionotidae is *Paracentrophorus*. It comes from the Lower Trias of Madagascar and according to his description it is more primitive than the earlier *Acentrophorus*. However, it has not accomplished the reduction of its tail from the heterocercal to the hemi-heterocercal state in the same manner as the rest of the Semionotids. With this in view I have redescribed the genus to try to ascertain its true relationship.

Genus ***PARACENTROPHORUS*** Piveteau, 1941

DIAGNOSIS. See Piveteau, 1941 : 77–88.

TYPE SPECIES. *Paracentrophorus madagascariensis* Piveteau.

Paracentrophorus madagascariensis Piveteau

(Text-fig. 66)

1941. *Paracentrophorus madagascariensis* Piveteau, p. 78, pl. 10, figs. 1–6 ; text-figs. 7–10.

DIAGNOSIS. As for genus.

SYNTYPES. The three specimens figured by Piveteau (1941, pl. 10) from the Lower Trias of Madagascar.

MATERIAL. Specimens in the B.M.N.H., from the Lower Trias of Bobasatrana, NE. Madagascar.

DESCRIPTION. *The skull.* In the skull the suprascapular is of normal proportions, but the extrascapular is broad and the parietals are large and squarish as in the Semionotidae. There is no median suprascapular (unlike *Acentrophorus*), and the dermopterotics are not as large as in *Acentrophorus* but they have the same rounded expansions of their outer borders anteriorly. The frontals are stout and of the same proportions as those in *Acentrophorus*, but are not completely fused, a distinct suture being visible. The frontals meet the paired nasals anteriorly. The nasals are stout ossifications, meeting in the mid-line, with the rostral, a small element between their anterior extremities and the premaxillae. The nasals bound a large nasal orifice anteriorly, while the antorbital completes the posterior edges. Of the shape of the premaxilla there is only very fragmentary evidence. The antorbital is a large bone somewhat hour-glass shaped, with a widened ventral area. The opercular is higher than broad, larger than the subopercular and the suture between them has the characteristic course, turning sharply upwards anteriorly. There is a distinct interopercular and the preopercular is narrow and gently curved. The preopercular has definitely not acquired the true Seminotid condition, where it is elongated in the lower region and extends far forward. In front of the preopercular are three recognizable suborbitals, the most ventral being the largest. The suborbital series is very similar to that found in the Amioidea. The maxilla is stout and long with a small supramaxilla at its posterior apex. There is a regular series of teeth along the length of the maxilla ; these are of medium size and pointed. The maxilla extends from just above the ventral extremity of the preopercular to the end of the orbit, where it meets the premaxilla. Along the anterior rim of the suborbitals are three infraorbitals and together with two more along the dorsal edge of the maxilla they bound the orbit behind and beneath. The dermosphenotic is large, much larger than in the Semionotidae generally, and probably represents the fusion of the dermosphenotic and supraorbital. There is only one supraorbital anterior to the dermosphenotic and there is apparently a gap between it and the succeeding antorbital. The mandible bears similar teeth to those of the maxilla, and beneath and behind the lower jaw is a complete set of branchiostegal rays, the most posterior rays being somewhat enlarged.

Sensory canals. The sensory canal system is as Piveteau (1941 : 81) described, except that I have been able to trace the infraorbital canal from the anterior corner of the dermopterotic, through the posterior extremity of the dermosphenotic and then round the infraorbitals into the antorbital. Here it gives off a branch dorsally which runs up through the length of the antorbital. The canal continues forwards probably into the rostral (this region is not clearly represented in any specimen) and back up through the nasal as the supraorbital canal.

Pectoral girdle and fin. The pectoral girdle is a stout ossification. From the suprascapular the supracleithrum runs back to midway down the opercular. Through the supracleithrum runs a continuation of the sensory canal system out on to the body scales as the lateral line. The cleithrum is large and stout and distinctly concave anteriorly. The primary pectoral girdle was not observed, but there are four stout radials on which the lepidotrichia of the pectoral fin articulated. Between the cleithrum and the supracleithrum is a single postcleithrum. All the above information was obtained by taking moulds in a plastic material called " Vinamould " from the original specimens in the B.M.N.H. (P 16245–6, P 19560–1, 62–3, 64–5, 70–1, 72–3).

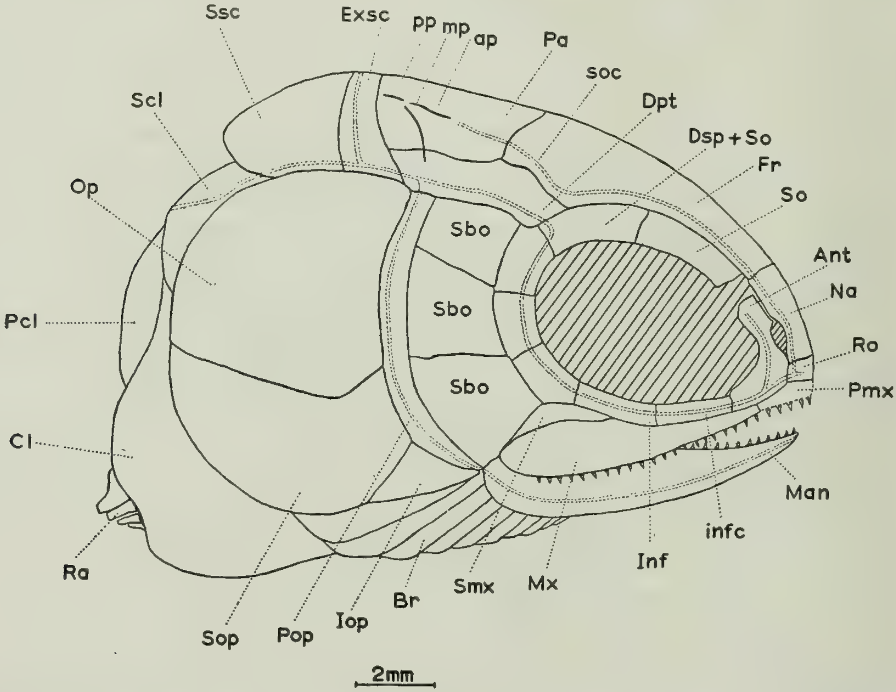

FIG. 66. *Paracentrophorus madagascariensis* Piveteau. Reconstruction of skull in lateral view.

From this description it is clear that *Paracentrophorus* is not at all closely related to either *Acentrophorus* or the later Semionotidae. The main differences in skull pattern include the nature of the preopercular, the unreduced maxilla and the stout nasals meeting in the mid-line in *Paracentrophorus*. Another major difference is the method of reduction of the heterocercy in the tail which is achieved in *Paracentrophorus* in the same way as in the Furid line. Minor differences include the absence of fin fulcra in *Paracentrophorus*, the position of the anal fin which is much nearer the tail in *Paracentrophorus*, and the somewhat high insertion of the pelvic fins. Further, unlike the Semionotidae the back is not depressed behind the insertion of the dorsal fin.

Thus there is a good case for putting *Paracentrophorus* in its own family the Paracentrophoridae and in placing this family not in the Semionotidae, as Piveteau (1941 : 77) has done, but in the Amioidea.

PHOLIDOPHOROIDEA

The next major group of Holostean fishes, the Pholidophoroidea, were those with the greatest evolutionary potential and from them arose the Teleosts, the dominant fishes of the present day. The earliest known Pholidophorid is alleged to come from the Middle Trias (Stolley, 1920 : 75), but Saint-Seine (1949 : 291) has cast doubt on this interpretation of a fish from the Muschelkalk of Germany. However, despite this, fragmentary remains for the most part referable to the genus *Pholidophorus* do come from Middle Trias deposits (*P. oblongus* Bellotti ; *P. obsoletus* Costa).

Stensiö (1932 : 164) has shown how the Pholidopleurids approach the Pholidophorids in structure, but indicates that the former group cannot be by any means considered ancestral to the latter. Further researches by Lehman (1952 : 145) into the structure of *Australosomus* has proved this to be correct, and it seems certain that the Pholidopleuridae represent a side branch, well off the main line of Holostean ancestry. Saint-Seine (1949 : 292) draws analogies between the Pholidophoridae and the Parasemionotidae, but concludes that the characters exhibited by the Parasemionotidae are too far removed from the condition found in the Pholidophoridae for direct descent to be possible. It has been shown below that there are many close resemblances between the families Parasemionotidae and Pholidophoridae, so much so that I have no hesitation in postulating the derivation of the Pholidophoridae direct from the earlier Parasemionotidae. The skull structure of the Pholidophoridae has long been considered similar to that of the Amiidae, but as Rayner (1937, 1948) has shown, the neurocrania differ considerably. If ancestry from the Parasemionotidae be accepted, these changes in the pattern of the neurocranial bones will have had time to have become apparent. A comparison of the Parasemionotidae with the Pholidophoridae is given below (p. 350) in tabular form (See also Text-figs. 67, 68):

From this comparison we see that the major differences between the two forms lie in first the preopercular and secondly the orbital series. The preopercular in *Thomasinotus divisus* Lehman (1952, fig. 129) (Text-fig. 62) is narrow and curved and contains the preopercular canal. It would need to become more curved anteroventrally and broadened in that region to approach the condition found in the

Pholidophorids. However, in front of this preopercular in *Thomasinotus divisus* there are three large plates acquired by the anamestic fragmentation of the anterior edge of the preopercular. In *Jacobulus novus* the anterior portion of the preopercular is similarly fragmented, only into two large plates. In both these genera the most posterior plate is the larger and contains both the supra- and postmaxillary sensory lines. In *Pholidophorus* sp. Westoll (1937, fig. 8, *d*) has shown that the most ventral plate of the circumorbital series (representing probably suborbital and infraorbital) has both these sensory lines present in it, and it appears probable that the large suborbitals in the Pholidophoridae have arisen by the anamestic fragmentation of the Parasemionotid preopercular. In *Leptolepis* and *Pholidophorus* there are five

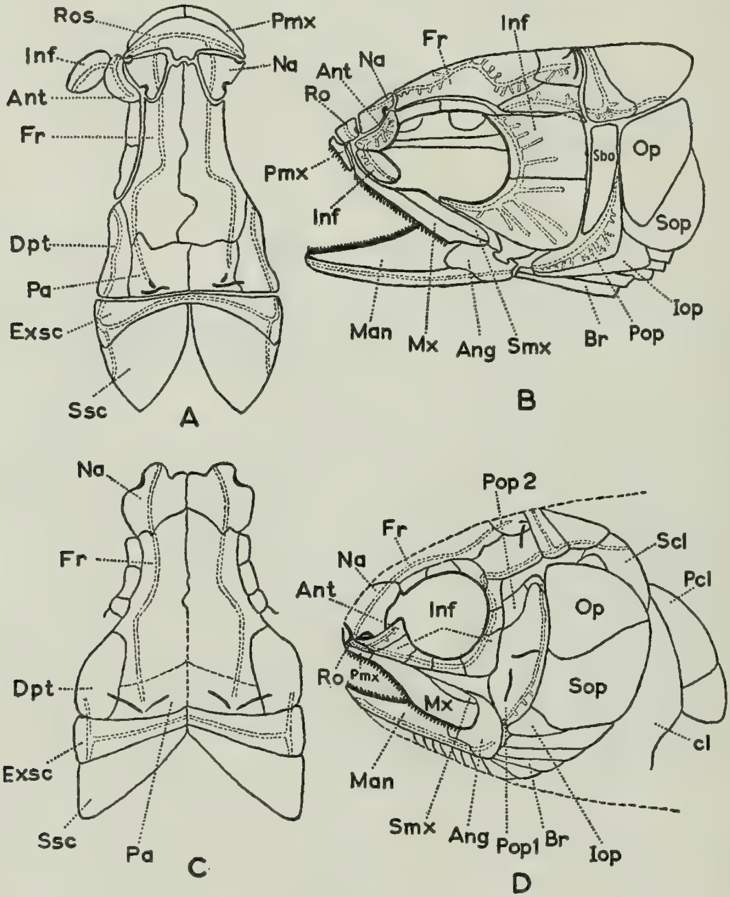
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FIG. 67. A, *Pholidophorus similis* Woodward, dorsal view of skull, after Saint-Seine (1949); B, *Pholidophorus similis* Woodward, lateral view of skull, after Saint-Seine (1949); C, *Jacobulus novus* Lehman, dorsal view of skull, after Lehman (1952); D, *Parasemionotus labordei* Lehman, lateral view of skull, after Lehman (1952).

infraorbitals, and of these the most posterior ventral is large and extends backwards over the anterior medial part of the preopercular (Text-fig. 68). Therefore it probably represents an infraorbital plate fused with one of the ventral suborbital plates. Beneath the eye in the Pholidophoridae the infraorbitals have become reduced to a narrow strip round the sensory canal, but this is a structural adaptation and is of no great importance. Schaeffer & Dunkle (1950 : 21) have shown the variation in the circumorbitals and suborbitals that can take place at the specific level within the genus *Pholidophorus* and this only adds further weight to the previous arguments. Further if the opisthotic in the neurocranium of the Amioidea is homologous with the autopterotic of the Pholidophoroidea, which is what I suspect, then a common

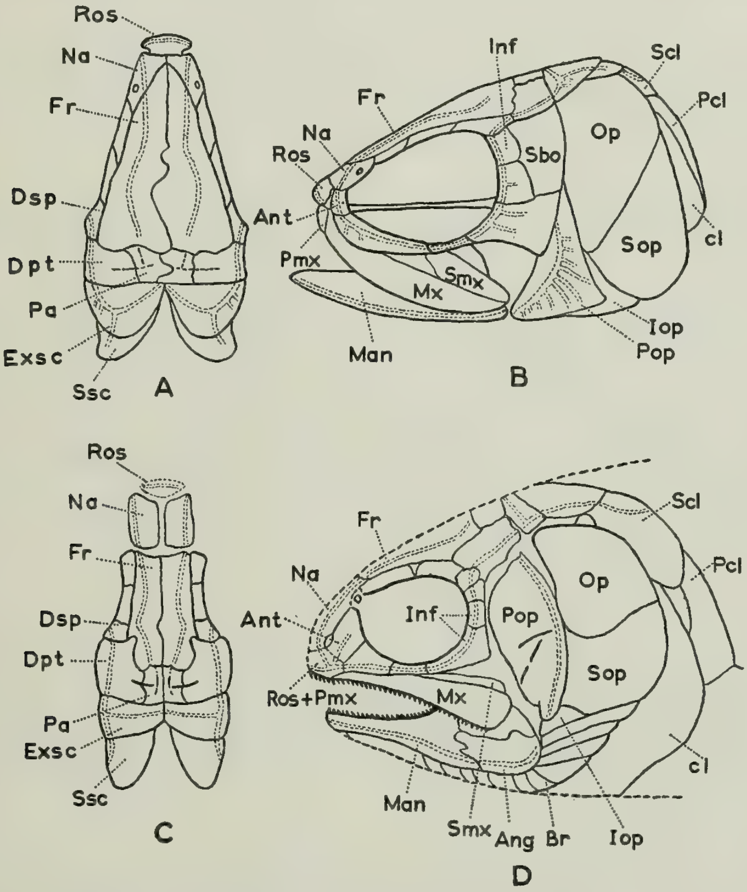
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Fig. 68. A, *Pholidophorus bechei* Agassiz, dorsal view of skull, after Rayner (1948) ; B, *Pholidophorus bechei* Agassiz, lateral view of skull, after Rayner (1948) ; C, *Watsonulus eugnathoides* (Piveteau), dorsal view of skull, partly after Piveteau (1934) ; D, *Watsonulus eugnathoides* (Piveteau), lateral view of skull, after Lehman (1952).

ancestry for both groups (from the Parasemionotidae) is even more certain. From all these facts it appears obvious that the Pholidophoridae have arisen directly from the Parasemionotidae.

In the superfamily Pholidophoridea I include the families Pholidophoridae, Leptolepidae, Protelopidae, Archaeomaenidae, Oligopleuridae and Pleuropholidae.

The progression Pholidophorid-Leptolepid-Teleost has been satisfactorily demonstrated by Rayner (1941, 1948) and Saint-Seine (1949); (see p. 316). Saint-Seine (1949 : 290–295) points out that while the Protelopids (*Eoprotelops*) specifically foreshadow the Teleost family Elopidae, the Leptolepids may be directly ancestral to the Chirocentridae.

Parasemionotid	Pholidophorid
1. Parietals small and squarish, median pit line long, extending well into the dermopterotic.	1. Parietals small and square, with a long median pit line, extending into the dermopterotic.
2. Dermopterotic larger than the parietal.	2. Dermopterotic of comparable size and shape to that of Parasemionotid.
3. Dermosphenotic small.	3. Dermosphenotic small.
4. Extrascapular narrow.	4. Extrascapular generally narrow.
5. Suprascapular enlarged, especially in *Watsonulus eugnathoides* (Text-fig. 68).	5. Suprascapular enlarged, especially in *Pholidophorus similis* (Text-fig. 67).
6. Rostral present with a rostral commissure.	6. Rostral and rostral commissure present.
7. Antorbital in *Watsonulus eugnathoides* and *Parasemionotus labordei* (Text-fig. 67) approx. bounds both nasal orifices ventrally, and has an upward branch of the sensory canal running through it (triradiate). This branch gives off several finer ones posteriorly.	7. Antorbital almost identical in size and shape and position. In *Pholidophorus similis* there is a comparable branch of the sensory canal (triradiate) with several finer posterior branches. Further, the antorbital more or less bounds the two nasal orifices ventrally.
8. Nasals large, rectangular, meeting in mid-line.	8. Nasals smaller, triangular and the nearest approach to their meeting in the midline can be seen in *Pholidophorus bechei* (Rayner, 1941) where they do still meet anteriorly (Text-fig. 68).
9. Maxilla completely free, and its posterior end has moved downwards. Supramaxilla present.	9. Maxilla comparable in shape and position, supramaxilla present.
10. Opercular slung well back, anterior ventral corner has moved upwards and backwards. The suture between it and the subopercular follows a characteristic course.	10. Opercular again similar, a little larger but slung upwards and backwards. The suture line between it and the subopercular follows a similar course to that in *Parasemionotus*.

11. Subopercular larger than opercular.	11. Subopercular slightly smaller than or of comparable size to the opercular.
12. Preopercular large, although undergoing anamestic fragmentation in some genera.	12. Preopercular very different in shape and position.
13. Interopercular present.	13. Interopercular present.
14. Circumorbital series complete, do not vary much in size.	14. Circumorbital series complete, some plates of which are very much expanded —others reduced.
15. Suborbital series just forming.	15. Suborbital series well developed.
16. Mandible composed of three bones.	16. Mandible has only two bones, surangular reduced.
17. Sensory canals well developed, the supraorbital canal running right back into the parietals.	17. Sensory canal system very similar, with the supraorbital canal passing right on to the parietal.
18. Cleithrum expanded ventrally, postcleithra present.	18. Cleithrum similar, single postcleithrum normally present.
19. Clavicles present.	19. Clavicles absent.
20. Gular plate present.	20. Gular plate present.

However, it would seem from the scale structure of *Pholidophorus* and *Leptolepis* that the progression Pholidophorid-Leptolepid-Teleost is not a strictly correct one. Although many of the Clupeoids, in particular the Chirocentridae, can be derived from a Leptolepid stock, such families as the Elopidae would on scale structure alone appear to have been derived more satisfactorily from a Pholidophorid ancestor. This idea of deriving some at least of the Teleosts direct from the Pholidophorids is not a completely new one. Woodward (1942 : 908) has already pointed out that the peculiar expanded ridge-scutes behind the pelvic fins of the Clupeoid *Diplomystus longicostatus* indicate a derivation from a Pholidophorid rather than a Leptolepid, since in the latter ridge-scutes are unknown. However the presence or absence of ridge-scutes is such a variable character that little importance can be attached to it. Again, the Salmonidae can be derived much more easily from a Pholidophorid ancestor than from a Leptolepid one, not just on scale structure, but on general skull disposition, in particular the make-up of the jaws which from the outset are far too specialized in the Leptolepids. Likewise the Characinidae probably also originated from an early Pholidophorid stock.

Thus the most primitive Teleost families can be straightforwardly derived from either the Pholidophorids or from the Leptolepids. One thing appears certain, they could not have been derived from any other known Holostean family, despite the opinion of Woodward (1942) to the contrary. I must agree with Rayner (1948 : 338) that from my own observations I can find no support in the morphology of the skull to derive the Teleost from any other source.

The Archaeomaenidae includes the genera *Archaeomaene, Aphnelepis, Aetheolepis* and *Madariscus* all described by Wade (1941*a*) from the Jurassic of Australia. This family bears a very close resemblance to the Pholidophoridae not only in the general shape of the body but in the construction of the skull, especially the lower and upper jaws. A few differences are apparent between, for example, *Archaeomaene* and *Pholidophorus*. In the former the vertebrae are ossified, resembling more the ring-like structure seen in some of the later Leptolepids, and there is a considerable variation in the circumorbital series. Despite these there is a close relationship between the Archaeomaenidae and Pholidophoridae, and they must have come from the same stock.

The two remaining families which I have included in the Pholidophoroidea for the sake of convenience, the Oligopleuridae and the Pleuropholidae present taxonomic difficulties. The Oligopleurids have been placed slightly off the Pholidophorid-Leptolepid line of evolution by Rayner (1941 : 232), but she indicates that they show numerous advances parallel to those of the Leptolepids. The high coronoid process, the fused vertebral elements, and thin scales are all similar to the former group, but the Oligopleurids still have fin fulcra and other peculiarities. The Pleuropholids are even further removed, but it seems probable that both these families took their origins from the same stock of the Parasemionotids that gave rise to the Pholidophorids.

SEMIONOTOIDEA

The third group of Holosteans is the Semionotoidea. The earliest member of this superfamily is the Permian genus *Acentrophorus*. The Semionotoidea do not constitute a major part of the Mesozoic fauna and did not give rise to other groups, owing to their early somewhat precocious specialization. Previously the Semionotids were believed to have given rise to all the later Holostean groups (Tate Regan, 1923; Gregory, 1923). Brough (1939 : 108) although excluding the Semionotids from the ancestry of the Furids, thinks that these two groups may have had a common ancestor in the Permian. Schaeffer & Dunkle (1950 : 18) support this view, pointing out that " It would appear less radical to derive a Semionotid from a Parasemionotid type than from any other known Palaeoniscid or Subholostean ". Schaeffer & Dunkle came to this conclusion after suggesting that both Gill (1923*b*, fig. 3) and Gregory (1933, fig. 21*b*) were wrong in their interpretation of the snout region of *Acentrophorus*, and that so far as it is known the Semionotid snout has a dermal bone pattern like that of the Parasemionotids. Because of this apparent discrepancy in interpretation it was decided to re-examine both *Acentrophorus* and *Semionotus*.

Genus *ACENTROPHORUS* Traquair, 1877

DIAGNOSIS. See Woodward, 1895*b* : 51 and Gill, 1923*b* : 20.

TYPE SPECIES. *Acentrophorus varians* (Kirkby).

Acentrophorus varians (Kirkby)

(Text-figs. 69, 70, 72)

1862. *Palaeoniscus varians* Kirkby, p. 267.
1864. *Palaeoniscus varians* Kirkby, p. 353, pl. 18, fig. 2.
1877. *Acentrophorus varians* (Kirkby) Traquair, p. 565.
1895*b*. *Acentrophorus varians* (Kirkby) : Woodward, p. 51.
1923*b*. *Acentrophorus varians* (Kirkby) : Gill, p. 19, figs. 1–3, 5, 7–11.
1933. *Acentrophorus varians* (Kirkby) : Gregory, p. 124, fig. 21*b*.
1939. *Acentrophorus varians* (Kirkby) : Moy-Thomas, p. 120, text-fig. 32*b*.

DIAGNOSIS. See Woodward, 1895*b* : 52 and Gill, 1923*b* : 20.

HOLOTYPE. Imperfect fish, Hancock Museum, Newcastle, from the Magnesian Limestone (Upper Permian), Durham.

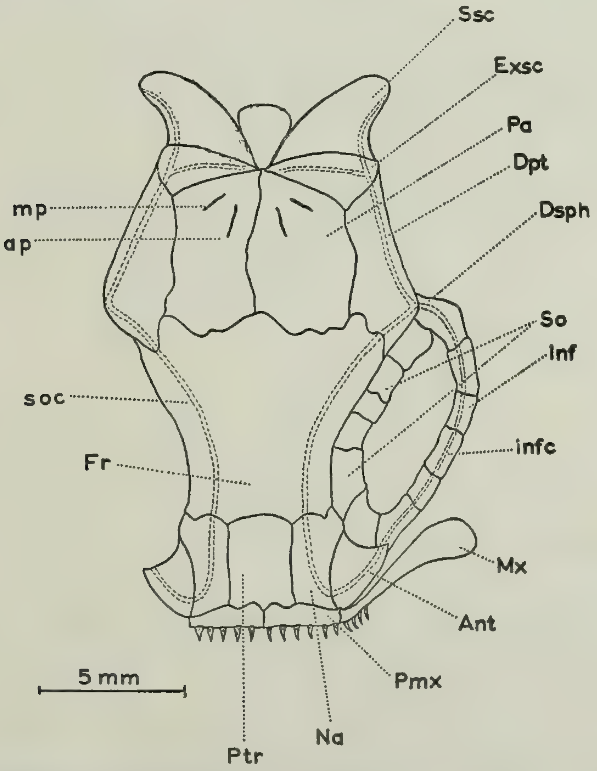

FIG. 69. *Acentrophorus varians* (Kirkby). Reconstruction of the skull roof in dorsal view, mainly from specimens P 593, P 594, P 597 in Professor Watson's collection.

Description. Through the kindness of Professor Watson I was enabled to examine a superb set of specimens of this genus contained in his collection. From these and from specimens in the B.M.N.H. a clear picture of the structure of the skull roof of *Acentrophorus* (Text-fig. 69) was built up. My own observations agree very closely with those of Gill (1923*b* : 25). The bones of the cranial roof are shown in Text-figs. 69, 70. The parietals are large, rectangular in shape and bear short median and anterior pit lines. The two parietals together form roughly a square over the neurocranium. On either side of the parietals are the somewhat elongated dermopterotics, roughly the same size as the parietals and having a rounded expansion of their outer borders anteriorly. The frontals are completely fused, and no suture line could be observed. They form a stout ossification, broad posteriorly, but narrowing between the orbits. Anteriorly the frontals abut a median, rectangular postrostral

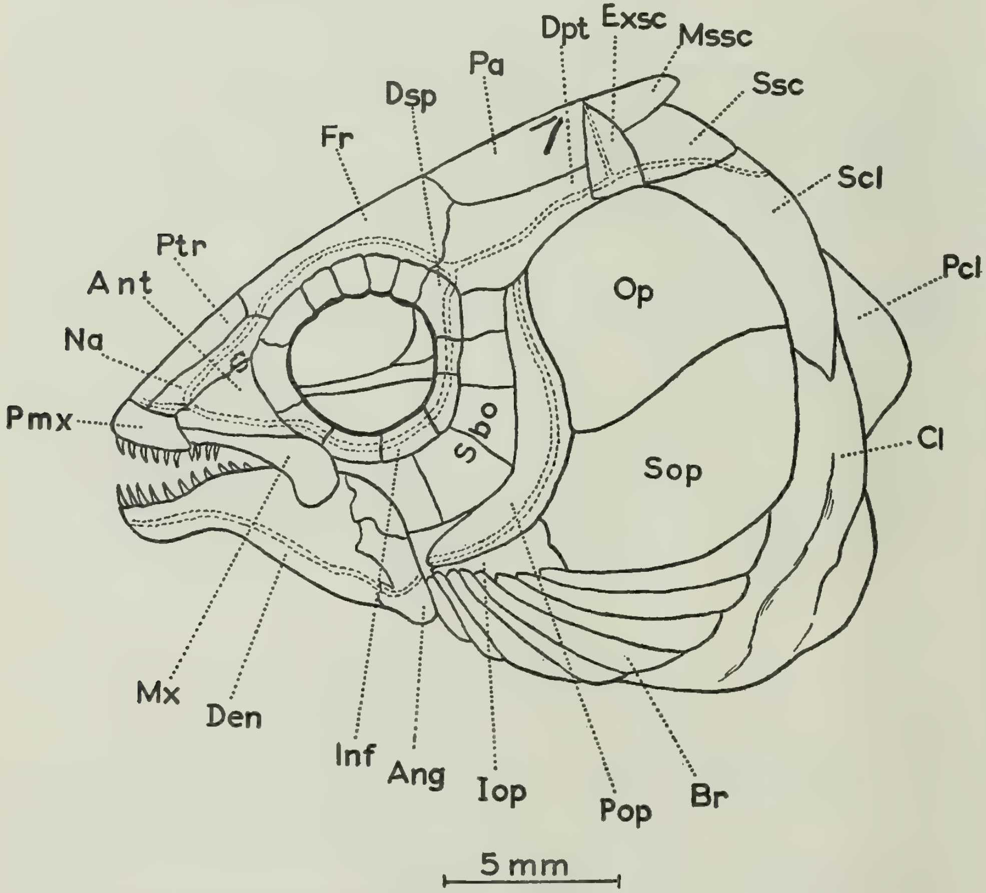

Fig. 70. *Acentrophorus varians* (Kirkby). Lateral view of skull, partly after Gill (1923*b*).

element (or possibly postrostral + rostral fused). The postrostral is a single, thin ossification showing no trace of a median division, and represents the paired nasals of Gill (1923*b* : 24) and the paired postrostrals of Gregory (1933, fig. 21*b*). On either side of the postrostral occur the nasals. These are a little smaller than the postrostral, and posteriorly articulate with the frontals, while anteriorly they meet the paired premaxillae. Fitting into the lateral edge of the nasal is a smaller triangular bone, the antorbital (rostral of Moy-Thomas, 1939, fig. 32*b*). The large orbit is surrounded by a chain of circumorbitals and a dermosphenotic, all of much the same size. Adjoining the hinder margin of the parietals is a pair of elongate, triangular extrascapulars, which do not quite meet in the mid-line. Behind the extrascapulars is a pair of well-developed suprascapulars, with a median element between them. The sensory canal system of the head is much as Gill described it (1923*b* : 28). The main cephalic division of the canal enters the posterior end of the suprascapular from the supracleithrum, and runs forward giving off the supratemporal commissure, which traverses the extrascapular, and then continues forward as far as the orbit, where it turns sharply downwards via the dermosphenotic, to form the infraorbital canal. The supraorbital canal joins the main cephalic division where it turns down as the infraorbital canal (i.e. in the dermopterotic) and then runs back through the frontal and nasal, curves sharply through the antorbital and links up again with the infraorbital canal. In the anterior postrostral region there were some traces of a rostral commissure, but this area was too crushed for definite interpretation.

Genus ***SEMIONOTUS*** Agassiz, 1832

Diagnosis. See Woodward, 1895*b* : 55.

Type species. *Semionotus bergeri* Agassiz.

Semionotus capensis Woodward

(Text-fig. 71)

1888*c*. *Semionotus capensis* Woodward, p. 138, pl. 6, figs. 1–5.
1895*b*. *Semionotus capensis* Woodward : Woodward, p. 58.
1901. *Semionotus capensis* Woodward : Schellwein, p. 1, pl. 1 ; pl. 2, figs. 1–4.
1909. *Semionotus capensis* Woodward : Broom, p. 262.
1915. *Semionotus capensis* Woodward : Hennig, p. 49, pl. 3.
1957. *Semionotus capensis* Woodward : Guffroy, p. 847, pl. 28 ; text-figs. 2, 3.

Diagnosis. A Semionotid of moderate size, fusiform in shape with a slender pedicle to the tail. Length of the head and opercular apparatus make up a quarter of the total body length. Dorsal fin arising in the middle of the back, which is depressed behind the point of insertion. Dorsal fin with approximately twelve lepidotrichia, the anal fin with less, approximately eight. Body scales smooth, not serrated.

Syntypes. Four nearly complete fishes on one block partly in counterpart, B.M.N.H. P 4089, from the Stormberg Beds, Ficksberg, Orange Free State.

Material. B.M.N.H. and Professor Watson's collection.

Remarks. A further study was made of this species from the Cave Sandstone

(Upper Triassic) to supplement that description of *Acentrophorus*, and to see whether or not the structure of the nasal region of *Acentrophorus* was unique amongst the Semionotidae.

Description. *The skull.* The parietals in this genus are large and square, with an anterior and posterior pit line near the posterior boundary (Text-fig. 71). The dermopterotic is smaller than in *Acentrophorus*, the frontals longer and not completely fused with one another. Anteriorly the frontals are pointed and have a V-shaped space between them into which the postrostral bone fits. The postrostral is much narrower than in *Acentrophorus* and is a very thin ossification. On each side of the postrostrals are the nasals and again these are smaller than in *Acentrophorus*. Between the nasals and the circumorbital series is one other smaller bone, an antorbital. The supraorbital series of bones totals five, whilst the infraorbitals together with the dermosphenotics number seven. There are four suborbitals of which the most posterior member is the largest. The second suborbital carries a groove in which lay the anterior division of the supramaxillary line : in the fourth suborbital a more vertical groove contained the postmaxillary line during life. The preopercular is very much curved ventrally and throughout its length runs the preopercular canal. The remainder of the skull and body is very close to Schellwein's (1901) description. The sensory canal system of the head, however, shows several differences from that described in *Acentrophorus*. The main cephalic division commences in the supracleithrum, runs through the supra- and extrascapulars, gives off the supratemporal commissure in the latter bone, runs across the dermopterotic and turns down through the dermosphenotic and carries on round the infraorbital series as the infraorbital canal. The supraorbital canal does not join the main

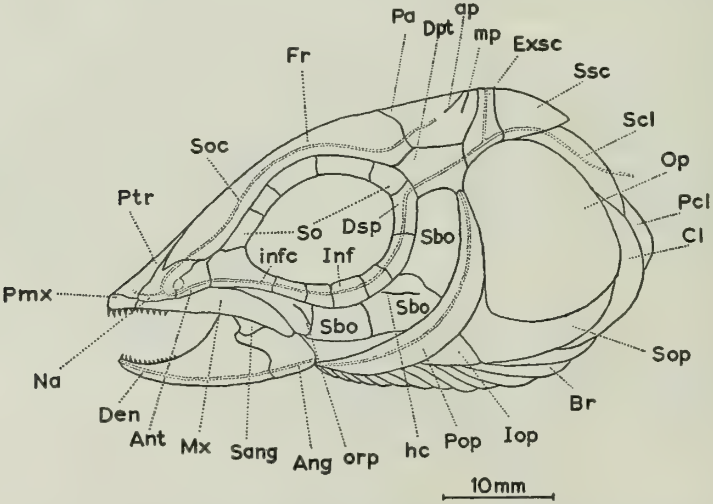

Fig. 71. *Semionotus capensis* Woodward. Reconstruction of skull in lateral view, mainly after B.M.N.H. P 10985, P 9486, P 6861 and P 4089.

cephalic division posteriorly, but commences in the parietal and runs down through the frontal, then into the nasal, where it turns sharply back into the antorbital to join with the infraorbital canal. There is just the semblance of a connection between the infraorbital and the supraorbital canals posteriorly, a line of irregular pores passing from the dermosphenotic to the supraorbital canal in the posterior frontal region. Where the sensory canal traverses the nasal it gives off a branch anteriorly, which passes forward into the postrostral. This represents the rostral commissure. The bone I have called the postrostral, from its position and extent, represents, then, a fusion of two elements, the rostral and postrostral. In *Acentrophorus* this ossification is large and separates the nasals widely. In the early Semionotids such as *Semionotus capensis* from the Cave Sandstone, this bone is reduced and posteriorly forms only a narrow strip separating the nasals (and overlies the posterior extensions of the premaxilla). Finally, in the later Semionotids such as *Lepidotes* and *Dapedium* it no longer separates the nasals but is reduced to a small ossification anterior to them. This small ossification is termed a rostral by Rayner (1948, fig. 10) and Schaeffer & Dunkle (1950 : 7), and is probably a correct interpretation, since the postrostral portion will have been the region to have undergone the reduction.

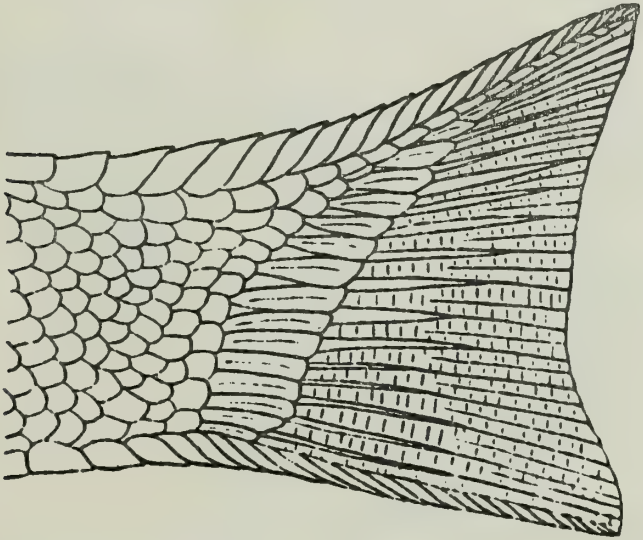

FIG. 72. *Acentrophorus varians* (Kirkby). Caudal fin. From Gill (1923*b*).

From these two descriptions it is obvious that the earliest Semionotid, *Acentrophorus*, differs markedly from the Parasemionotidae. In the Parasemionotidae the nasals are paired and meet in the mid-line, with a small rostral element between their anterior extremities and the premaxillae. The condition in *Acentrophorus* has already been described, wherein a large median postrostral completely separates the nasals. Turning to the circumorbital series, in the Parasemionotidae there are few bones, while in *Acentrophorus* there are as many as twelve. The remaining structures of the cheek are also quite different in the two forms. *Acentrophorus* already has a complete series of suborbital bones in the Permian, yet anamestic fragmentation of the preopercular has only just started in the Parasemionotidae by the Lower Triassic. Other major differences include the shape of the preopercular, which in *Acentrophorus* has already acquired the very specialized Semionotid condition, being distinctly curved and directed right forwards ventrally. The gape is consequently much shorter in *Acentrophorus*, and the lower jaw has moved forwards. Both the suprascapular and the dermopterotic are widened and enlarged. These points alone are sufficient to demonstrate that the two groups were derived independently from the Palaeoniscoidea, and further that their Palaeoniscoid ancestors were not at all closely related.

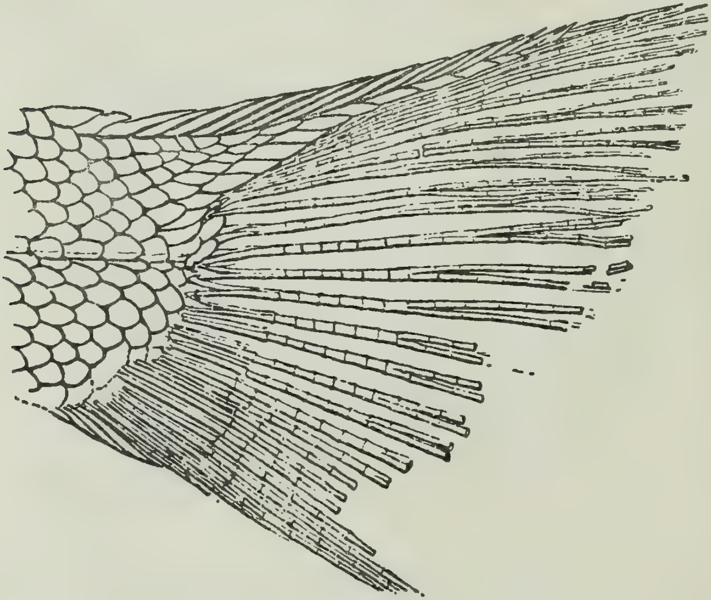

FIG. 73. *Dapedium orbis* Agassiz. Tail of a young individual. From Gill (1923*b*).

Other evidence for deriving the Semionotoidea direct from the Palaeoniscoids is to be found in the caudal region. The tail of *Acentrophorus* (Text-fig. 72) is completely heterocercal with the most dorsal row of scales complete, and extending to the tip of the tail. Gill (1923*b*, figs. 15, 16) has shown that in the Semionotidae this reduction of the tail from an ancestral heterocercal state to a hemiheterocercal form has taken place by the removal of longitudinal rows of scales from below upwards. *Acentrophorus* still retains the most dorsal row of scales complete, which extend to the tip of the tail, while in a young specimen of *Dapedium* (Text-fig. 73) Gill (1923*b*, fig. 16) has shown that the most dorsal row of scales was still prominent, extending about two-thirds of the distance to the tip. In the Parasemionotidae a different method was employed, the caudal lobe being reduced by the removal of transverse rows from the tip of the tail.

One final feature is the difference in the ossification of the neurocranium in the adult Amioid and Semionotid. In the Parasemionotidae the neurocranium of the mature individual is a single ossification in the postorbital region (Stensiö, 1932 : 227 ; Lehman, 1952 : 160), but in the Semionotidae (Rayner, 1948, fig. 30 and Text-fig. 74) this region is made up of discrete paired and unpaired ossifications. In *Lepidotes* (Text-fig. 44) the individual bones are distinct, and there was much cartilage present. In *Dapedium* the neurocranium is far more heavily ossified, although the individual bones can still be recognized (Text-fig. 39).

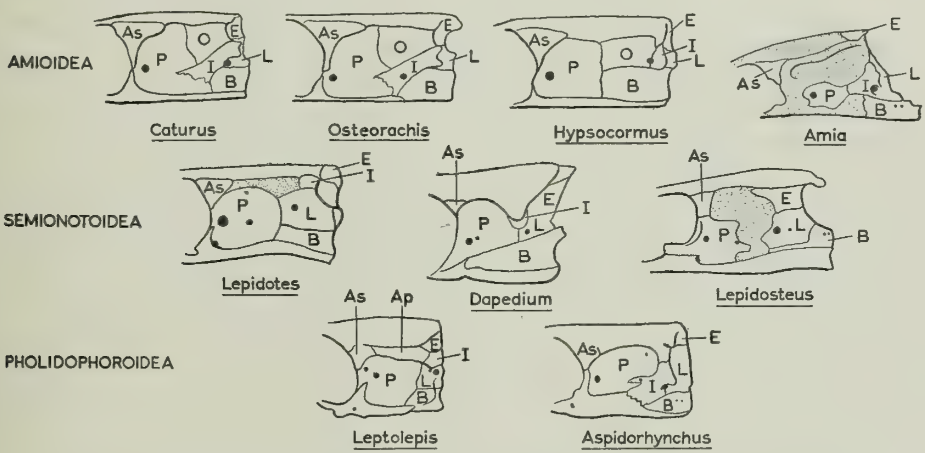

FIG. 74. Holostean neurocrania in lateral view, diagrammatic. *Leptolepis* and *Aspidorhynchus* from Rayner (1948).

In most of the adult Palaeoniscoids so far described in the literature, the postorbital region of the neurocranium is represented by a single ossification. However, in the immature specimen of *Cosmoptychius striatus* described by Watson (1928 : 49) the neurocranium shows several separate ossifications, whilst Westoll (1944 : 95) claims to have evidence of more than one ossification in a specimen of *Cheirolepis*. Other Palaeoniscoids described with separate neurocranial ossifications include *Birgeria* (Stensiö, 1921, 1937), *Elonichthys* (Rayner, 1948 : 331), and *Pteronisculus* (*Glaucolepis*, Nielsen, 1942 : 92). It is most probable then that the single ossification of the postorbital region of many of the adult Palaeoniscids and Subholosteans developed from several centres of ossification which have become completely fused.

Comparing now the structure of the neurocranium of the Semionotoidea with that seen in the Amioidea, none of the Semionotids so far described has an opisthotic present in its neurocranium whereas I have already established its presence (p. 286) in the Amioidea. Thus this absence of an opisthotic in the Semionotoidea separates them neatly from the Amioidea which possess this bone in at least the earlier members. There can be little doubt that the Amioidea and Semionotoidea arose from different Palaeoniscoid stocks.

Apart from the presence or absence of the opisthotic, the similar construction of the neurocrania in the Semionotoidea and Amioidea, and for that matter in the remainder of the Holostei, is due to the retention in the different ancestral stocks of a basic pattern present in the embryonic ossifications of a large number of Palaeoniscoids and Subholosteans. This view was put forward by Westoll (1944 : 95) and appears to be the only one by which the more or less homogeneous nature of the neurocrania within the Holostei (established by Rayner, 1948) can be explained.

The Semionotoidea range from the Upper Permian to Recent, and within the group several distinct evolutionary trends can be recognized. From the basic form, typified by *Acentrophorus* and *Semionotus*, one line has developed by deepening of the body and skull to give such forms as *Dapedium* and *Tetragonolepis*, while another has undergone elongation to give the very fusiform *Lepidosteus*.

The neurocranium of *Dapedium* has been described (Text-figs. 38, 39, 40), and it differs from that of *Lepidotes* in being much more solidly ossified and in possessing a supraoccipital. Woodward (1893 : 564) first recognized the presence of a supraoccipital in *Dapedium*, but Rayner (1948 : 307) disagrees with him, suggesting that the process called supraoccipital by Woodward is in fact the two outstanding mesial edges of the epiotics. The neurocranium of *Dapedium* (B.M.N.H. P 11189) used in the present description is small and probably of a young individual, and the supraoccipital is clearly apparent. Further, a supraoccipital can also be distinguished in a specimen of *Dapedium granulatum* from the Lower Lias of Lyme Regis (G.S. 60122). The neurocranium of *Dapedium* is drawn out dorso-ventrally in the posterior region and the supraoccipital appears to be a fresh development in order to fill in the posterior dorsal apex. Rayner (1948 : 334) has indicated that the supraoccipital in *Aspidorhynchus* and in the Pholidophorid-Leptolepid-Teleost line are not homologous and it is clear that neither of these is homologous with the supraoccipital in *Dapedium* (i.e., the difference in shape, size and extent in all these forms possessing it). In the only other Semionotoid neurocranium known, *Lepidosteus*, the condition is as in *Lepidotes* and the supraoccipital is absent.

Since the Semionotidae have evolved separately from the remainder of the Holostei, the question of the ancestry may be examined. Most authorities have expressed the opinion that there is no known Palaeoniscoid or Subholostean family that approaches that condition found in *Acentrophorus*. Westoll (1944 : 95) in contrast to these believes that there is strong evidence, which he does not publish, for deriving the Semionotids from the Palaeoniscoid family Elonichthyidae.

Elonichthys (Text-fig. 75) comes from the Carboniferous and is related to both *Gonatodus* and *Drydenius*, but differs mainly, as *Rhadinchthys* differs from *Mesopoma*, in the method of jaw suspensions. In *Gonatodus*, *Drydenius* and *Mesopoma* a more vertical suspensorium was acquired. Watson (1925 : 856 ; 1928 : 57) has demonstrated that in *Elonichthys caudalis* changes in the structure of the palate have already started and that the pterygoid has separated from the maxilla dorsally. In so doing the curious tube in which lay the *musculus adductor mandibulae* has disappeared, and, as Watson comments (1925 : 858) : " in this feature they [*Elonichthys*] have reached a condition which is found in all Holostei ". All that is necessary now is for the maxilla to become movable, and the suspensorium to straighten, and a true Holostean state of affairs would be in existence. Simultaneously with this freeing of the pterygoid from the maxilla, a close connection between the metapterygoid and the preopercular and hyomandibular was also established.

Secondly in *Elonichthys* the circumorbital series is represented by a ring of bones numbering eight in *Elonichthys serratus*. These then cannot be identified individually with the ring of five which make up the circumorbital series of the majority of Palaeoniscoids, *Coccocephalus, Canobius, Mesopoma, Rhadinichthys*, etc. Thus we have a Palaeoniscoid with a series of orbital bones much larger in number than is the normal condition in the Palaeoniscoidea ; as Watson comments, " the division of the orbital bones foreshadows that in the Semionotidae ".

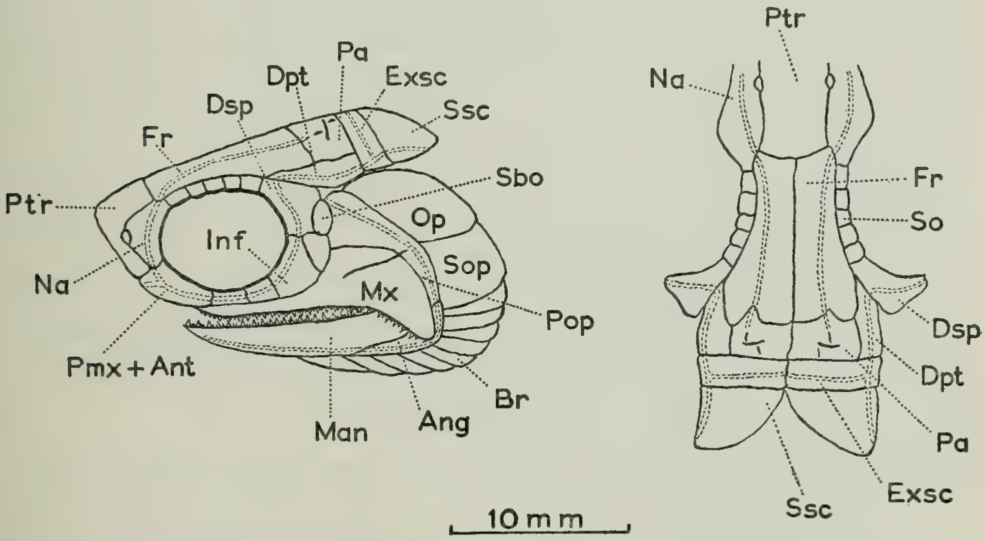

FIG. 75. *Elonichthys serratus* Traquair. Restoration of skull in dorsal and lateral views, from Moy-Thomas & Dyne (1938).

Thirdly, between the posterior circumorbitals and the anterior rim of the preopercular is a series of suborbital bones, three in *Elonichthys caudalis*, two in *Elonichthys serratus* (Text-fig. 75). These could quite easily provide the source for the suborbitals of the Semionotidae.

Fourthly, the supraorbital canal in *Elonichthys caudalis* ends in the frontal and does not pass on into the parietal ; in this respect Watson indicates that it may show a condition intermediate between the normal Palaeoniscoid and that of *Oxygnathus*. In this respect it could also be intermediate between that of the normal Palaeoniscoid and *Acentrophorus*.

Fifthly, *Elonichthys* shows a limited development of ridge scales similar to that condition found in *Acentrophorus*, and lastly, *Elonichthys* still has its full complement of branchiostegal rays, and they are not reduced as in *Mesopoma*.

From the above facts it is clear that although *Elonichthys* is a long way off that grade of organization seen in *Acentrophorus*, it does show changes of the right nature. It is quite unlikely that the family Elonichthyidae is ancestral to the Semionotoidea but until new forms are found (from the Lower Permian) which establish clearer relationships, then as far as can be seen they are about the only family from which the Semionotoidea could be derived.

ASPIDORHYNCHOIDEA

The fourth group of Holosteans to be dealt with, the Aspidorhynchoidea, includes the single family Aspidorhynchidae. This family ranges from the Middle Jurassic to the Upper Cretaceous. In it are included two closely-allied genera, *Aspidorhynchus* and *Belonostomus* (Text-fig. 76). Both these genera are highly specialized on their first appearance, possessing elongated bodies and snouts, and deepened flank scales. In *Aspidorhynchus* the rostrum is produced well beyond the mandibular symphysis, but in *Belonostomus* (Saint-Seine, 1949, fig. 114) the rostrum is only just longer than the mandible. The skull roof in both genera is typically Holostean and there is a dermosphenotic in *Belonostomus tenuirostris*, although Rayner (1941 : 229) indicates that it is missing or fused with the frontals in some species of *Aspidorhynchus*. In contrast the extrascapular is seemingly absent in *Belonostomus*. There is only one series of bones (three in number) between the eye and the preopercular in *Belonostomus*, and these represent the fused suborbitals and posterior infraorbitals, since a sensory canal runs round the anterior rim of the series. The condition of the cheek plates and the preopercular is almost identical to that condition found

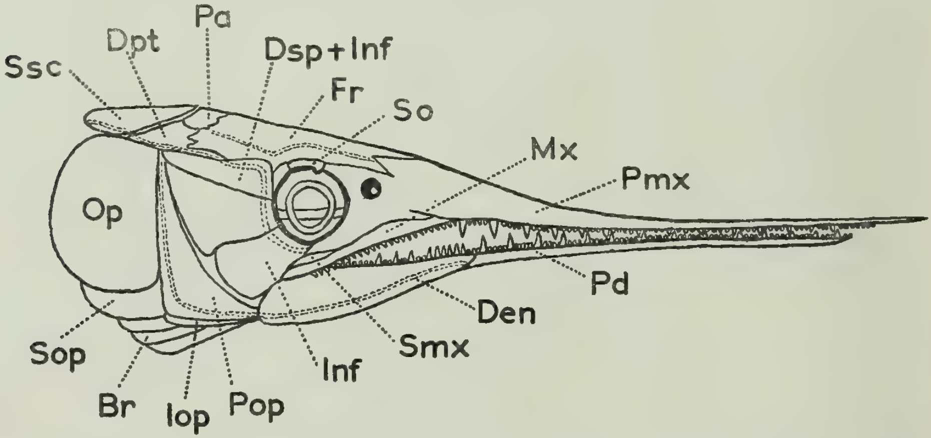

FIG. 76. *Belonostomus tenuirostris* Agassiz. Restoration of skull in lateral view, after Saint-Seine (1949).

in *Pholidophorus*. Other points of similarity between the Aspidorhynchoidea and the Pholidophoroidea include the absence of the basipterygoid process, the similar mobile maxilla with a supramaxilla attached, and the composition of the lower jaw, where in both the surangular is missing.

The neurocrania of the Aspidorhynchoidea and the Pholidophoroidea exhibit several differences. In both there is a supraoccipital, but in the former it is a very small bone and has nothing like the extent of the corresponding bone in the Pholidophoroidea. The intercalar is reduced in the Pholidophoroids, while the lateral occipital stretches round underneath it to form part of the wall in the posterior postorbital region (Text-fig. 74). In the Aspidorhynchids the intercalar is large and constitutes a considerable portion of the wall of the neurocranium in the median postorbital region (Text-fig. 74). In conclusion, the Pholidophorids are peculiar in having an autopterotic in the neurocranium (although as I have already indicated, it is probably homologous with the opisthotic of the Amioids) while the Aspidorhynchids have an opisthotic but this is only present in early ontogeny.

So we see that the Aspidorhynchoidea share a number of characters in common with the Pholidophoroidea, but because of their highly specialized state when they first appear, it is difficult to classify them with the Pholidophoroidea. Westoll (1949 : 95) suspects a relationship between the Aspidorhynchoidea and the Triassic Saurichthyidae and Pholidopleuridae, but both these groups are highly specialized in themselves, and I can see no evidence whatsoever for even the remotest connection.

In the last instance I feel loth to postulate an entirely separate evolution for the Aspidorhynchoidea, so tentatively until new forms are found, I link them with the ancestral Pholidophoroid stock.

PYCNODONTOIDEA

Finally, in the grade Holostei, I include the superfamily Pycnodontoidea. The earliest known Pycnodont, *Eomesodon hoeferi*, comes from the Upper Trias of Hallein, Salzburg, and the family continues until the Eocene when it dies out.

In general organization the Pycnodonts are Holostean and superficially resemble the contemporary Semionotid, *Dapedium*, but this is entirely due to similar modes of life. The appendicular skeleton of the Pycnodont is quite distinct from that of the Palaeoniscoids, but identical to that of the majority of the other Holostei. The fins are unmistakably Holostean with the dorsal and anal fins closely resembling those of *Dapedium*—the rays being equal in number to their supports—and the tail is hemiheterocercal. However, the Pycnodonts show many features which cannot be reconciled with the more conservative Semionotid or Furid condition ; the much expanded preopercular, the unusual pattern of the skull roof with a median supraoccipital and the short Palaeoniscoid-like parasphenoid (Woodward, 1939 : 609). Other respects in which the Pycnodonts differ from the remainder of the Holostei include the unossified vertebral centra, the cheek plates (where present) reduced to tesserae, the almost complete reduction of the branchiostegal rays, the minute fin fulcra and the reduction of scales on the caudal region. Thus the

Pycnodonts must represent a quite separate and independent evolution from other Holostean groups.

A Comparison of the Pycnodonts with the Platysomida

Since the Pycnodonts show no real similarity to any other Holostean family, the question of their ancestry requires examination. Woodward (1939 : 608) considers that the Pycnodonts have been directly derived from the Platysomids. In doing so he assumes that " a highly specialized type of Chondrostean has evidently passed into a still more specialized type of Holostean ". This view is untenable if one considers the well-marked differences between the two groups.

Moy-Thomas & Dyne (1938), Moy-Thomas (1939) and Dyne (1939) have shown that within the Platysomida there are at least two distinct lineages, the Amphicentridae and the Platysomidae. From their evidence it is probable that the Platysomids are polyphyletic in nature, but for convenience in discussion the two families will be treated as one group, the suborder Platysomida, except where otherwise stated.

In the Pycnodonts the roof of the mouth is occupied by the so-called " vomer ", which bears several rows of rounded crushing teeth, which oppose a similar series set on the splenial bone. This formidable dentition is nowhere encountered in the Platysomidae, but is paralleled in several members of the Amphicentridae. The cleithra differ in the two groups (Pycnodonts and Platysomida) and there are no clavicles in the Pycnodonts. The dorsal and anal fins in the Pycnodonts are supported by only one set of radials instead of the two sets in the Platysomida, and the fin-rays in the Platysomida are more numerous than the distal set of radials (or baseosts). Fin fulcra are present in the Platysomida, the branchiostegal apparatus is complete, and the tail heterocercal.

The affinities between the two groups include a persistent notochord, the similarity in the scales and scale distribution, the presence in at least one species of *Platysomus* of a dorsal lateral line besides the median lateral one, the general shape of the head and the prognathic snout. Most of these points were enumerated by Traquair (1879 : 382), but in view of the differences it is impossible to derive the Pycnodonts direct from the Platysomida despite their similarities.

A Comparison of the Platysomida with the Bobasatraniidae

Woodward (1939 : 608) further proposed that partial links between the Pycnodonts and the Platysomida are provided by the Lower Triassic family, the Bobasatraniidae. The Bobasatraniidae do in fact resemble the later Pycnodonts, but could not themselves be direct derivatives of the Platysomida. White (1932 : 83) considered the Bobasatraniidae to be directly derived from the Palaeoniscids rather than from the Platysomids, but following Stensiö (1932) and Lehman (1957) it is more reasonable to assume that the two groups (Bobasatraniids and Platysomids) are closer and that from a basic Platysomid-like stock both the Bobastraniidae and many Platysomids have been evolved. In view of the possible polyphyletic nature of the Platysomida, it is more probable that the Bobasatraniids came from the basal stock of the family Amphicentridae than from that of the Platysomidae.

Similarities between the Bobasatraniidae (Text-fig. 77) and Platysomida include the general shape of the head and body, and the make-up of the shoulder girdle. The two sets of radials supporting the dorsal and anal fins, the axonosts of which are expanded, compressed and sinuous and in contact with one another in both forms (Westoll, 1944). The distribution of the cheek plates is similar and the preopercular has at least two ossifications along the preopercular canal in the Bobasatraniids and in the two Platysomids, *Platysomus gibbosus* (Westoll, 1941 : 47) and *Platysomus parvulus* (Moy-Thomas, 1939, fig. 30*a*). Westoll (1941 : 47) points out the strong resemblances shown in the shape, distribution and ornamentation of the squamation between *Platysomus gibbosus* and *Bobasatrania*. Further, the peculiar development of paired, arcuate tubules from the main lateral line in *Bobastrania* is also found in *Platysomus gibbosus*. In the cheek region the maxillary portion of *Bobasatrania* is easier to associate with that of the family Amphicentridae than it is with the Platysomidae, in both the Bobasatraniids and the Amphicentrids teeth being missing on the maxilla.

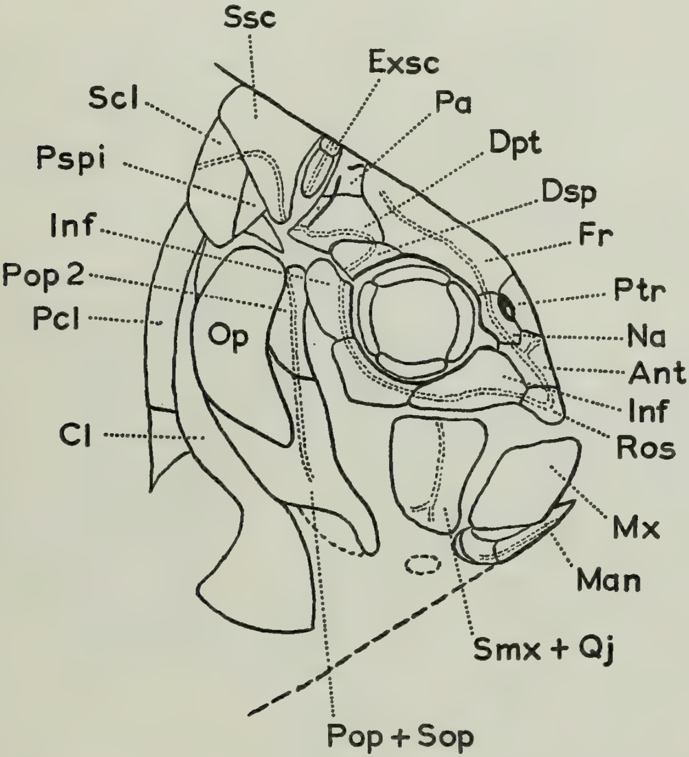

FIG. 77. *Bobasatrania mahavavica* White. Skull in lateral view, after Lehman (1956).

Dissimilarities between the Platysomids and the Bobasatraniids include the

Holostean-like structure of the median fins of the latter. The axonosts and baseosts in the median fins very nearly correspond in number in *Platysomus*, whereas in the Bobasatraniids the baseosts are more numerous than the axonosts and are almost equal to the lepidotrichia. The opercular apparatus is very different in the Bobasatraniids, having a ventral preopercular plate below and beneath the opercular and a much reduced opercular. Other major differences include the complete reduction of the branchiostegal rays in Bobasatraniids and the ventrally broadened cleithrum with no clavicle present.

A Comparison between the Bobasatraniidae and the Pycnodontidae

The Bobasatraniidae and the Pycnodontidae bear many similarities, but the very specialized nature of the former rules out the possibility of a direct descent for the Pycnodonts from the Bobasatraniids, as Woodward (1939 : 608) postulated. However, there is little doubt that both groups originated from the same basic stock.

The similarities between the Bobasatraniids and the Pycnodonts are numerous, and all those features of *Bobasatrania* which are alien to the Platysomids agree with the condition found in the Pycnodonts. The structure of the fins of the Bobasatraniids corresponds with that of the Pycnodonts, and the opercular apparatus is very similar in the two groups. In both there is an almost complete reduction of the branchiostegal rays, and neither group possesses a clavicle. Perhaps the most important similarity between the Bobasatraniidae and the Pycnodontidae so far not mentioned in the literature is the presence of at least two ossifications along the preopercular canal in both families. The present author has shown that the small bone above the preopercular in *Eomesodon liassicus* (Text-fig. 51) carries a portion of the sensory canal and therefore must be considered as a preopercular plate. This division was also seen (with the canal) in *Mesodon macropterus* and *Coelodus costae.*

Other similarities between the Bobasatraniidae and Pycnodontidae include a backwardly-inclined hyomandibular, devoid of an opercular process. [However, Woodward (1895*b* : 193) records an opercular process for *Gyrodus* in a position similar to that of the other Holostean groups and to the Teleosts.] Again the hyomandibular articulation is identical, there being a symplectic between the hyomandibular and the quadrate in both groups and there seems to be some provision for movement between the symplectic and the quadrate, a condition also observed in *Dorypterus*. The courses of the sensory canals are very similar on the head bones of the Bobasatraniidae and the Pycnodontidae, and are in all essentials of the Palaeoniscoid-Platysomid type in both. The lateral line of the Pycnodonts still retains the ventral tubule of the arcuate pair (Text-fig. 53) and has a dorsal division similar to that of the Bobasatraniids and some Platysomids. There are large ridge scales in front of the dorsal and ventral angles in both the Pycnodonts and Bobasatraniids. The shape and structure of the scales are similar, both forms having scales higher than broad, with well-developed peg-and-socket articulations. The scales are characterized by their rhombic shape and by a fairly strong ridge on the anterior part of the median side. The lepidotrichia of the Bobasatraniids become rather separate and resemble more closely the condition found in the Pycnodonts rather than that found in the Platysomids. An unusual post-abdominal bone is found in the Bobastraniids and in some Pycnodonts (e.g. *Gyrodus frontalis*), but this bone also occurs in the Platysomids and in *Dorypterus*. The mandibles of the two groups are not so alike, and Dunkle & Hibbard (1946) have shown that the mandible of *Micropycnodon* is more like that found in the Platysomids than in the Bobasatraniids.

Other peculiarities of the Bobasatraniids include an increase in size of them axilla and premaxilla, the former being absent in the Pycnodonts and the latter reduced, the loss of the pelvic fins and the presence of a more or less complete squamation. The axial and fin skeletons are also different ; in the Pycnodonts the neural and haemal spines are joined to the neural arches and there is but a single row of fin supports. Westoll (1941 : 48) suggested that these last differences " may be due to the structural needs of the developing fish ", and this probably applies to the scales as well. These and other differences point to the fact that the Pycnodonts could not have been directly derived from the Bobastraniids, but most probably came from the same Palaeoniscoid stock, the same stock that gave rise to the Amphicentridae.

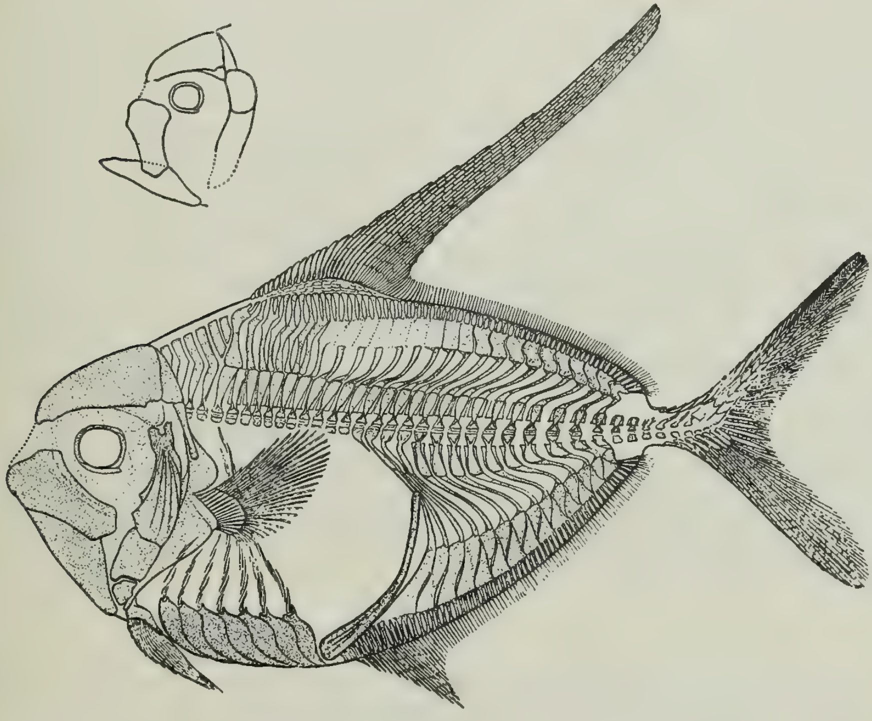

FIG. 78. *Dorypterus hoffmani* Germar. From Gill (1925).

Summing up all the evidence, it is clear that from a Platysomid-like ancestral stock both the Amphicentrids and the Bobastraniids evolved. The line leading to the Bobasatraniids later dividing to give on the one hand the Bobasatraniidae and on the other the Pycnodontidae (Text-fig. 79).

Dorypterus *Compared with the Bobasatraniids, Platysomids and Pycnodonts*

Mention must be made of another closely-allied genus, *Dorypterus* (Text-fig. 78). There are close relationships between the axial skeleton and fin skeleton of *Dorypterus* and *Bobasatrania* (e.g. the expanded, sinuous axonosts in contact with one another in both genera), and in the development of the body axis of the caudal fin. The heterocercal tail is modified by a thinning and weakening of the body lobe in *Bobasatrania* and is similar to the condition found in *Dorypterus* (Westoll, 1941 : 42). The bones of the upper jaw are similarly developed in both, and the pectoral girdles show many likenesses. Despite these few similarities there are many divergent features ; no known Bobasatraniid, or Platysomid for that matter, shows the extreme modifications of the skull found in *Dorypterus* (Gill, 1925 : 643 ; Westoll, 1941 : 39). Likewise, the body of *Dorypterus* is not completely covered with thick scales as in the Bobasatraniids or Platysomids. The scaling is reduced to the anterior portion of the trunk, and in this respect *Dorypterus* resembles the Pycnodonts. Westoll (1941 : 48) describes the condition found in the Pycnodont *Mesodon* and points out the close similarity between the nature and the extent of the scaling of it and *Dorypterus*. He also points out that the presence of additional scales on the caudal lobe of *Dorypterus* is paralleled by similar scales on the reduced caudal lobes of *Microdon* and *Mesodon* (noted by Woodward, 1918 : 52, 64). However, these features, as Westoll correctly recognized (1941 : 48), do not prove a close relationship between the Pycnodonts and *Dorypterus*, since they are probably concerned with similar adaptations in the two forms (e.g. reduction in body weight, stabilization in the vertical plane).

From the evidence it is clear that *Dorypterus* is much more closely related to the Platysomids and the Bobasatraniids than to the Pycnodonts. The Dorypterids and Bobasatraniids must have come from the same early Platysomid-like stock, the two lines diverging, the Bobasatraniid line eventually giving rise to both the Bobasatraniids and the later Pycnodonts, whilst the Dorypterid line soon died out.

IV. CONCLUSIONS

From the previous discussion it is clear that the Holostei do not form a natural order but include families derived from different Palaeoniscoid stocks. These derivatives happen to share similar but independently acquired characters, such as construction of the cheek, opercular apparatus, fins, appendicular skeleton and the reduction of the heterocercal tail. Many of these characters have also been independently acquired by several other groups which do not quite reach the Holostean grade of evolution (e.g. *Ptycholepis*, *Haplolepis*, *Aeduella*), but which come under Brough's (1936, 1939) category of Subholostei.

Both the orders Holostei and Subholostei include forms derived from different Palaeonisciform stocks, and as such represent grades of evolutionary development rather than natural, monophyletic orders. Therefore the retention in the classification of the orders Subholostei and Holostei should be abandoned, since not only do they cut across phyletic lines but, as Westoll (1944 : 96) states, " they are based on characters which are of adaptational nature ". In this respect I agree with

Westoll and his work may be consulted for further discussion on the subject. In spite of abandoning the status of the two groups as orders, the terms "Holostei" and "Subholostei" can for the time being at least be usefully retained for convenience in discussion, for although purely arbitrary they have become through general usage associated with a certain grade of organization.

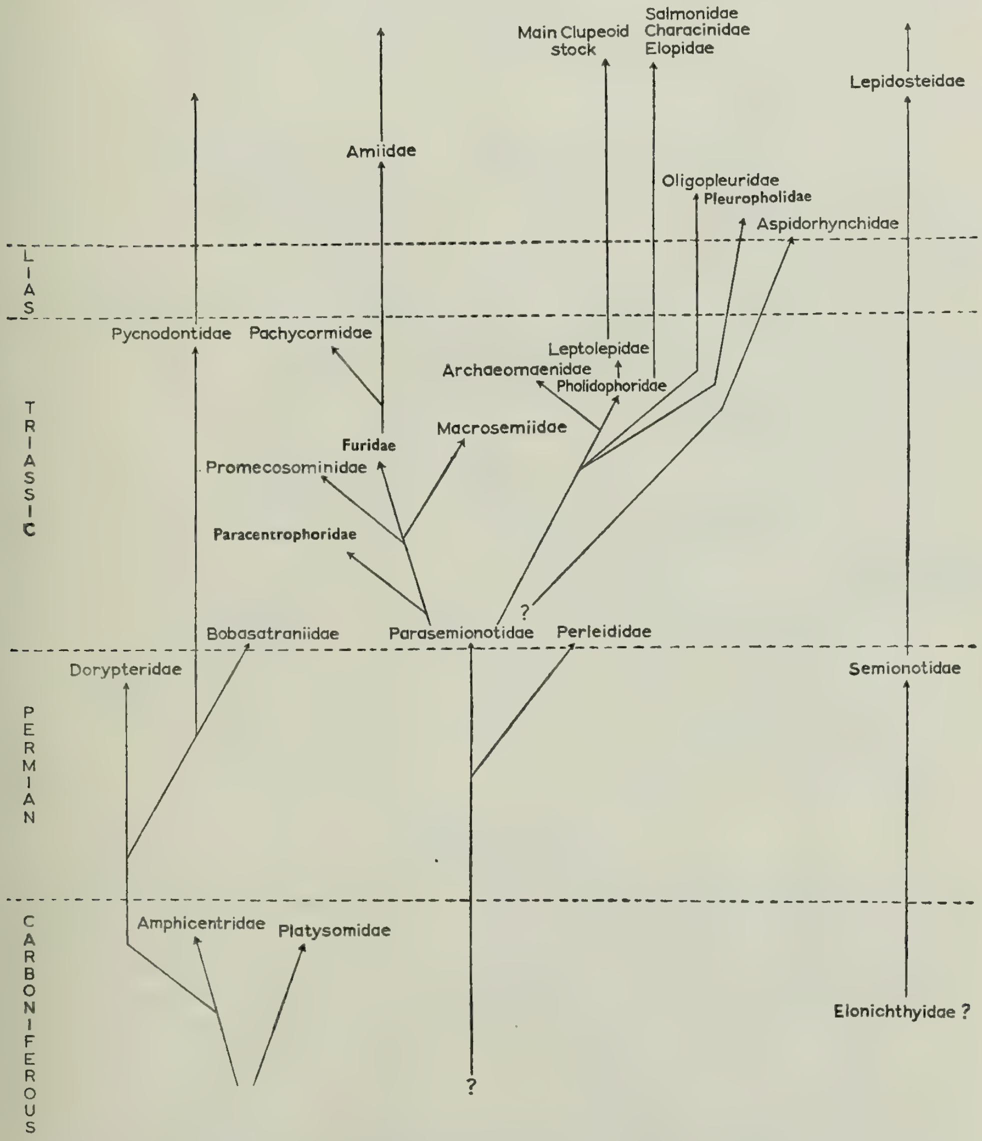
Salmonidae
Characinidae
Elopidae
Main Clupeoid stock
Lepidosteidae
Amiidae
Oligopleuridae
Pleuropholidae
Aspidorhynchidae
LIAS
Pycnodontidae
Pachycormidae
Leptolepidae
Archaeomaenidae
Pholidophoridae
TRIASSIC
Macrosemiidae
Furidae
Promecosominidae
Paracentrophoridae
?
Bobasatraniidae
Parasemionotidae
Perleididae
Dorypteridae
Semionotidae
PERMIAN
CARBONIFEROUS
Amphicentridae
Platysomidae
Elonichthyidae ?
?

FIG. 79. Evolutionary tree of the main Holostean groups.

In conclusion, the arrangement of the families included in the term Holostei by previous authors is set out below and superfamily designation is given to the individual groups.

" *HOLOSTEI* "

Group I. Amioidea

i. Furidae.
ii. Amiidae.
iii. Macrosemiidae.
iv. Pachycormidae.
v. Promecosominidae.
vi. Paracentrophoridae.

Group II. Pholidophoroidea

i. Pholidophoridae.
ii. Leptolepidae.
iii. Oligopleuridae.
iv. Pleuropholidae.
v. Archaeomaenidae.
vi. Protelopidae.

Group III. Aspidorhynchoidea

i. Aspidorhynchidae.

Group IV. Semionotoidea

i. Semionotidae.
ii. Lepidosteidae.

Group V. Pycnodontoidea

i. Pycnodontidae.

" *SUBHOLOSTEI* "

This term embraces a variety of forms which resemble the Palaeoniscoids, but which also show various progressive structural trends towards that grade of organization termed Holostean. The order Subholostei, as I have already indicated, should be abandoned, since it is essentially a horizontal classification, but the retention of the term Subholostei is necessary for the time being at least, for ease in discussion.

Three of the genera I have described from the Lower Lias of Lyme Regis come within the meaning of the term Subholostean, in that they all show developments from the Palaeoniscoid condition towards the Holostean one.

The first genus described is *Platysiagum*, which is placed in the family Platysiagidae. *Platysiagum* is the single genus and contains the Middle Triassic species *Platysiagum minus* (Brough, 1939 : 14) and the Lower Liassic *Platysiagum sclerocephalum* (Text-fig. 13). Brough (1939 : 17) has already pointed out that this genus, although superficially Palaeoniscoid, has departed in many respects from the Palaeoniscoid plan. The paired fins and the hemiheterocercal tail are distinctly Holostean in nature, while the lower jaw has a pronounced coronoid process on it. There is an incipient interopercular, the suspensorium is upright and the maxilla partly freed from the preopercular. The affinities of the family are vague, there being no other Subholostean or Holostean with which it could be linked. As Brough (1939 : 17) concludes, it is merely the representative of another Palaeoniscoid line which has moved independently towards the Holostean grade of structure.

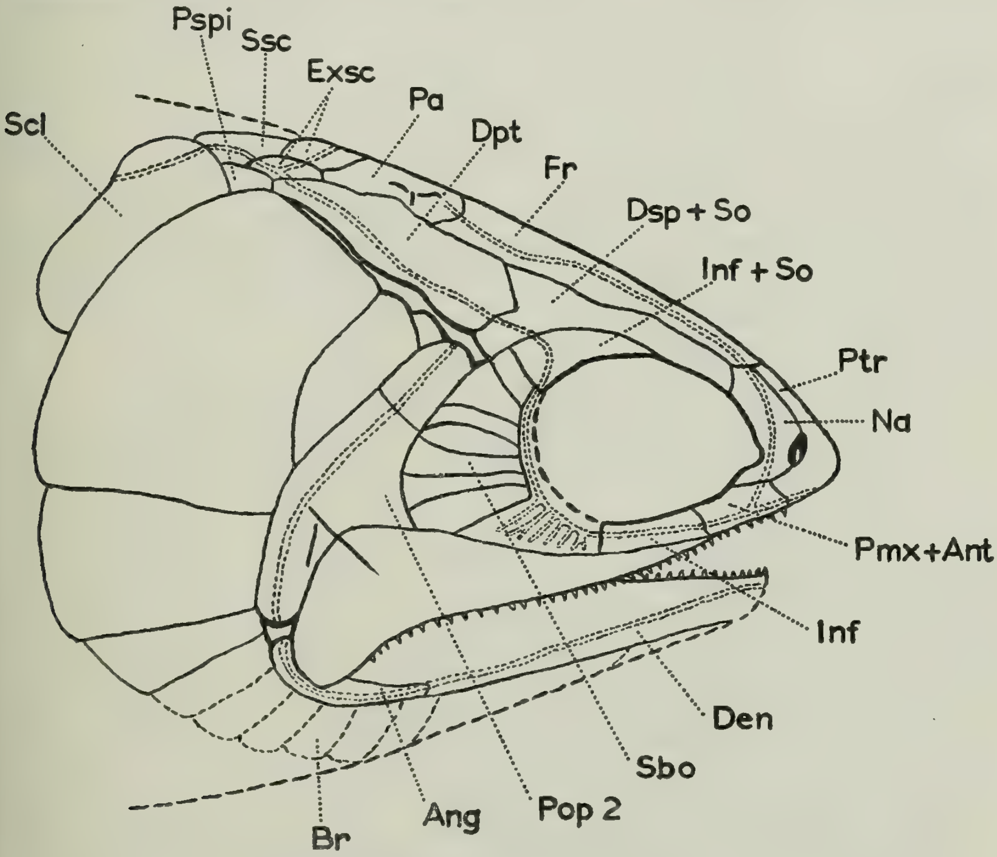

FIG. 80. *Boreosomus gillioti* Priem. Lateral view of skull, after Lehman (1952).

The second genus dealt with is *Ptycholepis*. This genus had for a long time been considered Holostean and placed in the Furidae (Eugnathidae, Woodward, 1895*b*: 316). However, the works of Brough (1939 : 98) and Aldinger (1937) have shown that *Ptycholepis* is not a Holostean, and that it must be regarded as the representative of yet another independent line from the Palaeoniscoids. Both these authors agree that the Ptycholepids have been derived from the Palaeoniscoid *Boreosomus* (Text-fig. 80), with which they share many points of similarity.

The earliest Ptycholepid is *Ptycholepis barboi* (Brough, 1939 : 58) from the Middle Trias of Besano. I have redescribed the Lower Lias species *Ptycholepis monilifer* and the Upper Liassic *Ptycholepis bollensis*. In *Ptycholepis bollensis* (Text-fig. 17) the sensory canal system of the head was well shown, and the true homologies of the postorbital bones recognized. These postorbital bones clearly represent the posterior infraorbitals which have grown back over the preopercular, since the infraorbital sensory canal passes through their anterior edges. Moreover, the small bone termed a supramaxilla by Brough (1939, fig. 30) is in fact a member of the infraorbital series, since through it also the infraorbital canal passes.

The third and last genus described is *Saurorhynchus*. It belongs to the family Saurichthyidae, which according to Stensiö (1925 : 175) contains two genera, the first *Saurichthys*, into which all the Triassic forms are placed, and the second *Saurorhynchus*, which embraces the two Liassic species *Saurorhynchus acutus* (Agassiz) and *Saurorhynchus brevirostris* (Woodward). Stensiö (1925 : 175) states that *Acidorhynchus* (*Saurorhynchus*) differs from *Saurichthys* in the following respects :

> " (1) Smaller lengthening of the rostrum.
> (2) No or very slight ganoine ornamentation.
> (3) Certain differences in the shape and relations of the dermal bones.
> (4) Rather much reduced opercular.
> (5) Absence of vertical striations on the teeth basally of the enamel cap."

One further difference, according to both Woodward (1895*b* : 10) and Stensiö (1925 : 176) is the ossification of the neurocranium, which in *Saurorhynchus* is degenerate and cartilaginous.

Most of these differences have now been shown to be invalid. The first, " the smaller lengthening of the rostrum " is incorrect, because from a series of measurements made on all the Saurichthyids and Saurorhynchids in the B.M.N.H. the resultant graphs (Text-fig. 81) and calculations showed that there was no significant difference in the relative length of the rostrum in *Saurichthys* and *Saurorhynchus*. The second difference, " no or very slight ganoine [enamel] ornamentation ", is also invalid, several specimens of *Saurorhynchus* having skull bones distinctly ridged and tuberculated with enamel. The third difference noted by Stensiö, " the differences in the shape and relations of the dermal bones " is, however, correct, the maxilla and preopercular in particular being quite distinct in shape and size. The rather reduced opercular is also a recognizable difference, the opercular rarely extending far below the ventral limit of the preopercular. However, the " absence of vertical striations on the teeth basally of the enamel cap " is incorrect, for on some teeth of *Saurichthys* these striations are absent, whilst on others of *Saurorhynchus* they are present (Text-fig. 22). Lastly, the neurocranium is ossified in *Saurorhynchus*, although not so heavily as in the earlier Saurichthyids. The neurocrania differ in one or two respects : the cranio-spinal process is not so wing-like in *Saurorhynchus* as in *Saurichthys*, the myodome not so deep and the parasphenoid extends much further forward along the base of the rostrum than in *Saurichthys*.

These differences are sufficient for separating the Liassic species, *S. acutus* and *S. brevirostris*, from the remainder of the Saurichthyids, and for putting them in a separate genus, *Saurorhynchus*, as Stensiö (1925 : 175) proposed.

The relationships of the Saurichthyidae have been exhaustively dealt with by Stensiö (1925 : 207) and it only remains for me to emphasize that they form a

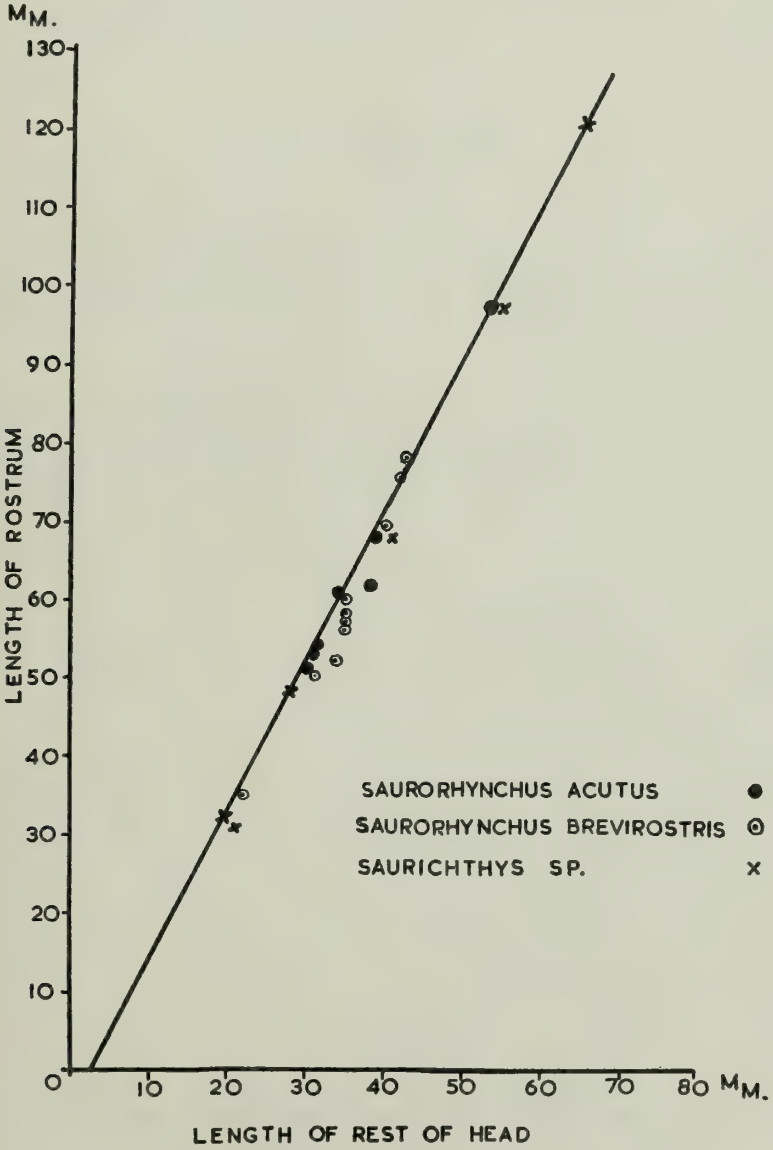

FIG. 81. Graph of length of rostrum against length of rest of head.

degenerating series closely related both to the Palaeoniscoids and to the Sturgeons (Acipenserids, Chondrosteids and Polydontids).

In conclusion, mention must be made of the genus *Browneichthys*. This genus is known from one fragmentary fossil from the Lower Lias of Barrow-on-Soar, Leicestershire, and now in the Leicester Museum. Woodward (1895*b* : 23) provisionally associated it with the Saurichthyids under the name of *Browneichthys ornatus*. From its unique scale pattern I find it difficult to classify it with the Saurichthyids, a view already put forward by Griffith (1958 : 159).

PALAEONISCOIDEA

The Palaeoniscoids have an exceedingly long range in the geological time scale, extending from the Middle Devonian until the Cretaceous. During that time many of the lines developed independently towards the Holostean grade of organization. However, one or two of the families were more conservative in nature, and retained the Palaeoniscoid structure practically unaltered right through until the Jurassic and Cretaceous.

One such family is the Coccolepidae. This family contains the single genus *Coccolepis* and ranges upwards from the Lower Lias (*Coccolepis liassica*) to the Wealden of Belgium (*Coccolepis macroptera*). In addition it has a very wide geographical distribution, members of the genus being recorded from England, Belgium, Turkestan, Russia and New South Wales. It contains the last members of the Palaeoniscoidea and culminates in the Lower Cretaceous. The Lower Liassic species *Coccolepis liassica* shows little advance in structure over such Devonian forms as *Cheirolepis* and *Stegotrachelus*. It still retains a very oblique suspensorium and there is no suborbital series developed, but the nasal region has become a little modified by the loss of the overhanging rostrum and the formation of a premaxilla.

Another genus from the Lower Lias of Lyme Regis is *Centrolepis*. It contains the single species *Centrolepis aspera*, which previously was placed provisionally first in the Palaeoniscoidea by Woodward (1891 : 520) and then in the Palaeoniscoidea or Subholostei *Incertae Sedis* by Romer (1945 : 580). From my description there is no doubt that the genus correctly belongs with the Palaeoniscoidea. The structure and disposition of the skull roofing bones are very similar to that condition found in *Rhadinichthys* (Lower Carboniferous). Apart from the absence of a " dermohyal " in *Centrolepis aspera*, the remainder of the skull is strikingly similar, including the two suborbitals, the opercular apparatus, the make-up of the pectoral girdles and the cheek and snout regions. *Centrolepis* is very much larger than *Rhadinichthys*, being almost three times as long, and it has several peculiarities including the branching of the sensory canal system anteriorly. The normal Palaeoniscoid condition is for the infraorbital canal to branch in the rostral bone and give off an anterior branch that passes into the postrostral. In *Centrolepis aspera* (Text-fig. 5) the infraorbital canal does not branch until it is in the nasal bone. Added to this is the distinct nature of the scales and the relative position of the fins. From these differences it is obvious that the Centrolepids represent a rather isolated lineage and there is every cause for placing the genus *Centrolepis* in a family of its own, the Centrolepidae.

The remaining Palaeoniscoid from the Lower Lias of Lyme Regis is *Oxygnathus*. This genus has been more or less completely described by Woodward (1890 : 431) and Watson (1925 : 867 ; 1928 : 58). It has been correctly placed by Romer (1945 : 579) in the family Palaeoniscidae, and bears many similarities with earlier members of this family. Such forms as the Triassic *Glaucolepis* and the Permian *Palaeoniscus* are quite comparable with *Oxygnathus* in general structure of the skull and make-up of the body.

The three Liassic Palaeoniscoids described all represent end lines which have managed to survive comparatively unchanged from the Palaeozoic, and which eventually succumb to the far better adapted Holosteans and Teleosts.

COELACANTHIFORMES

The Coelacanthidae range from the Lower Carboniferous to the present. Woodward (1891 : 398) showed that the skeletal characters exhibit little variation; and that " it is difficult to recognize differences sufficiently marked to be regarded as justifying the subdivision of the family into a series of genera ". He points out that the arrangement and proportions of the fins are practically constant, and that the supplementary caudal is the only variable element.

Stensiö (1921 : 119) agrees with Woodward, although he states that there is a rather greater variability than we have been inclined to think, and also that the general characters as a rule are somewhat more strongly marked than was thought to be the case by a number of authors.

The genus I have described from the Lower Lias of Lyme Regis is *Holophagus gulo*, and it is a large fish with a prominent supplementary caudal fin. The isolated pterygoid-quadrate plates described from the Stonesfield Slate are doubtfully of *Holophagus* but their structure shows a considerable amount of variability.

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LETTERING USED IN TEXT-FIGURES

$\left.\begin{array}{l}a\\a_1\\a_2\end{array}\right\}$ processes on the ossified primary girdle plate.
Ang, angular.
Ant, antorbital.
Ant.+ Ptr. antorbito-postrostral.
aort, canal for dorsal aorta.
Ap, autopterotic.
ap, anterior pit line.
Art, articular.
asc. ps, ascending process of parasphenoid.

B, basioccipital.
Bbr I, basibranchial I.
Bbr II, basibranchial II.
Bhy, basihyal.
bpt. pr, basipterygoid process.
Br, branchiostegal ray.
Bsph, basisphenoid.

can.W, canals of Williamson.
Cbr. I, ceratobranchial I.
Cbr II, ceratobranchial II.
Cbr III, ceratobranchial III.
Cbr IV, ceratobranchial IV.
Chy, ceratohyal.
Cl, cleithrum.
Clav, clavicle.
Co.pr, coronoid process.
Cor, coronoid.
Cora, coracoid.
Crpsph, crista on parasphenoid.
c.sp, cell space.

d, depression.
Den, dentary.
Despl, dentalo-splenial.
d.l.l,. dorsal lateral line.
Dpt, dermopterotic.
Dpt+Exsc, dermopterotic-extrascapular.
Dsp, dermosphenotic.
Dsp + Inf, infraorbito-dermosphenotic.
Dsp+So, supraorbito-dermosphenotic.
d.t, dentinal tubule.

E, epiotic.
e, enamel (ganoine).
Ectpt, ectopterygoid.
eff.ps.art, efferent pseudobranchial artery.
Enpt, entopterygoid.
Excl, extracleithrum.
Exsc, extrascapular.
ext.car, foramen for external carotid artery.
ext.sc, external semicircular canal.

f, foramen.
f.a, articulatory facet.
fac.art.pal, articulatory surface for the autopalatine.
fac.f, facial foramen (recess).
fh, fenestra hypophyses.
f.hym, facet for hyomandibular.
f.m, foramen magnum.
f.na, facet for neural arch.
Fr, frontal.
fuls, fulcral scale.

Gu, gular plate.

Hbr I, hypobranchial I.
Hbr II, hypobranchial II.
Hbr III, hypobranchial III.
Hbr IV, hypobranchial IV.
hc, supramaxillary sensory line.
Hhy, hypohyal.
h.la, horizontal bone lamellae.
hsp, haemal spine.
Hym, hyomandibular.

I, intercalar.
Inf, infraorbital.
infc, infraorbital sensory canal.
Inf+So, infraorbito-supraorbital.
int.car, foramen for internal carotid artery.
Iop, interopercular.
Ir, interrostral.

L, lateral occipital.
lc, cephalic division of main lateral line.
Lep, lepidotrichia.
l.l, lateral line.

Man, mandible.
mc, mandibular sensory canal.
m.cor.arch, mesocoracoid arch.
Meck, ossified Meckelian cartilage.
Metpt, metapterygoid.
Mix.t, mixicoronoid teeth.
mp, median pit line.
Mssc, median suprascapular.
Mx, maxilla.
myod, myodome.

n_1, anterior nasal aperture.
n_2, posterior nasal aperture.
*N*a, nasal.
Na + Ant, nasalo-antorbital.
nc, neural canal.
not, notochordal pit.
ns, neural spine.
nt, aperture for notochord.
Nu, neural arch.

o, opisthotic
o, pore.
occ.n, foramen for occipital nerve.
Op, opercular.
op.pr, opercular process.
Orb, orbit.
orp, postmaxillary sensory line.
Orsp, orbitosphenoid.
Oss.Prg, ossified primary pectoral girdle.

P, prootic.
p, parapophysis for rib.
Pa, parietal.
Pa+Dpt, parieto-dermopterotic.
Pal, palatine.
Pcl, postcleithrum.
Pd, postdentary.
Pmx, premaxilla.
Pmx+Ant, premaxillo-antorbital.
Pmx-Ros, rostralo-premaxillary.
Po, postorbital.
Po.inf, postorbito-infraorbital bone.
Pop, preopercular.
popc, preopercular canal.
Pop.Po, preoperculo-postorbital.
Pop.Quj, preoperculo-quadratojugal.
Pop+Sop, preoperculo-subopercular.
por, postorbital process.

pp, posterior pit line.
Ppg, primary pectoral girdle.
Pra, preangular.
Prcs, cranio-spinal process.
prof, foramen for profundus.
Psph, parasphenoid.
Pspi, postspiracular.
Pt, pterygoid.
Ptr, postrostral.
Ptsph, pterosphenoid.
Pvg, pelvic girdle.

Qu, quadrate.
Quj, quadrato-jugal.

Ra, radials.
ram.dors, foramen for branches of the ramus ophthalmicus superficialis trigemini.
ros, rostral.
r.ot, foramen for the ramus oticus.
r.s, ridge scale.
Rsc, dorsal ridge scute.

Sang, surangular.
Sbo, suborbital.
s.br, side branches.
Sc, scale.
s.c, sensory canal.
Scap, scapula.
Sc.f, scapular foramen.
Scl, supracleithrum.
Scom, supratemporal commissure.
Scr, sclerotic ring.
Smx, supramaxilla.
Smx+Qj, supramaxillo-quadratojugal
So, supraorbital.
soc, supraorbital sensory canal.
Socc, supraoccipital.
Sop, subopercular.
Sp, splenial.
Spt, suprapterygoid.
Ssc, suprascapular.
Sty, stylohyal.
Sym, symplectic.

$\left.\begin{array}{l}t_1\\ t_2\\ t_3\end{array}\right\}$ teeth of lower jaw.
tem.gr, temporal groove.
trig.fac.ch, trigemino-facialis chamber.

vas, vascular groove.
v.can, horizontal network of canals.
vert. cart. ant, vena cerebralis anterior.

Vo, vomer.
Vo.t, vomerine teeth.
v.t, ventral tubule.

w, widening of lateral line.

$\left.\begin{matrix}x_1\\x_2\end{matrix}\right\}$ bones of opercular series.

I, olfactory canal.
II, optic foramen.
III, foramen for oculomotor nerve.
IV, foramen for trochlear.
V, foramen for trigeminal nerve.
V.VII.op.sup, foramen for superficial ophthalmic branches of trigeminal and facial nerves.
VI, foramen for abducens.
VII, foramen for facial nerve.
VII.hym, foramen for hyomandibular branch of facial nerve.
VII.buc, foramen for buccal branch of facial nerve.
VII.pal, foramen for palatine branch of facial nerve.
VII. ot, foramen for otic branch of facial nerve.
IX, foramen for glossopharyngeal nerve.
IX.st, foramen for supratemporal branch of glossopharyngeal nerve.
X, foramen for vagal nerve.

B.M.N.H., British Museum (Nat. Hist.)
G.S., Geological Survey Museum.
Ox. M, University Museum, Oxford.
R.S.M., The Royal Scottish Museum, Edinburgh.
Sedgw. M., Sedgwick Museum, Cambridge.

MUSEUM HISTORY

PLATE 36

Ptycholepis monilifer Woodward

Block 1, showing lower jaw and ceratohyal. B.M.N.H. 39868.

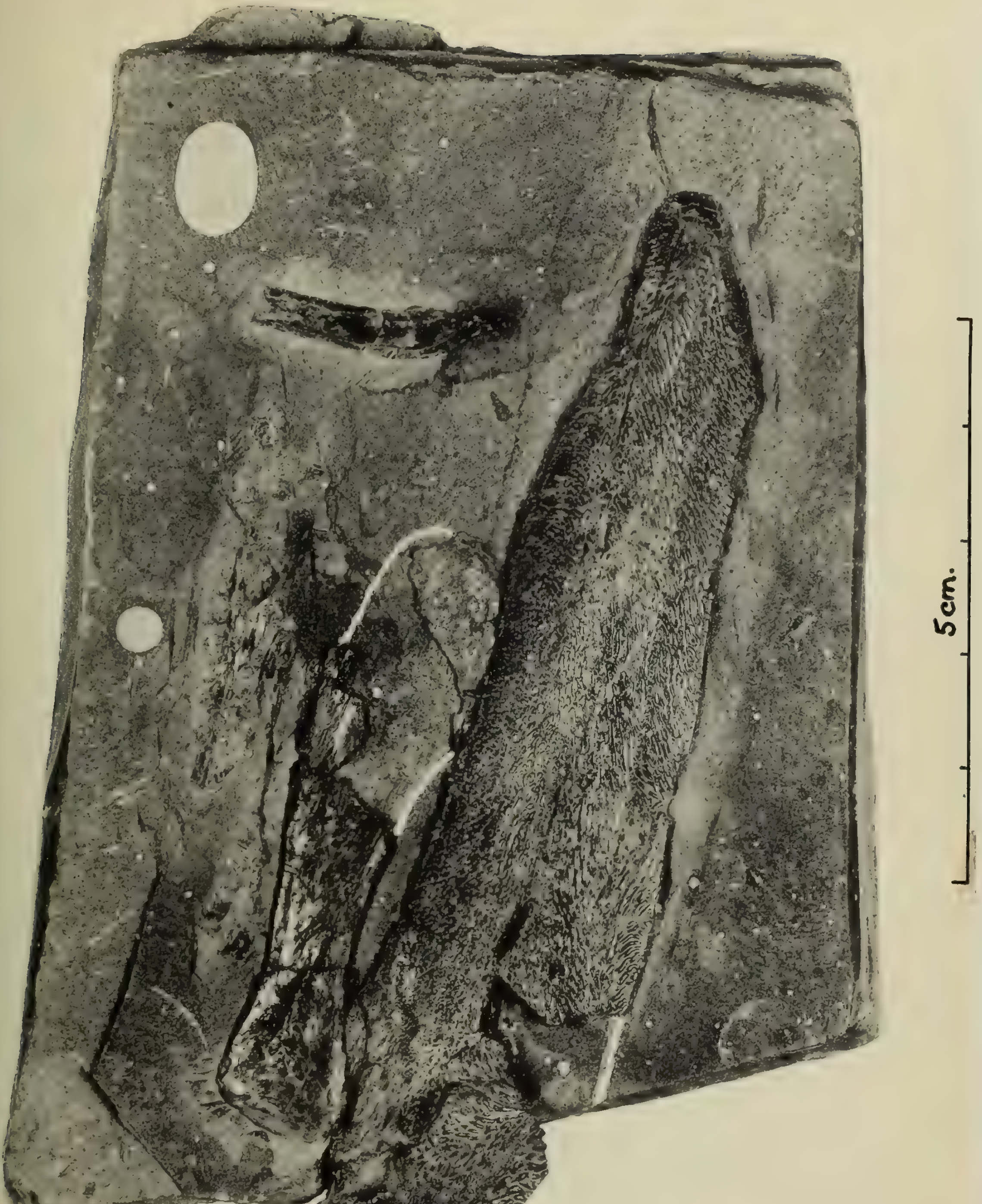

5cm.

PLATE 37

Ptycholepis monilifer Woodward

Block 2, showing maxilla and branchiostegal rays. B.M.N.H. 39868.

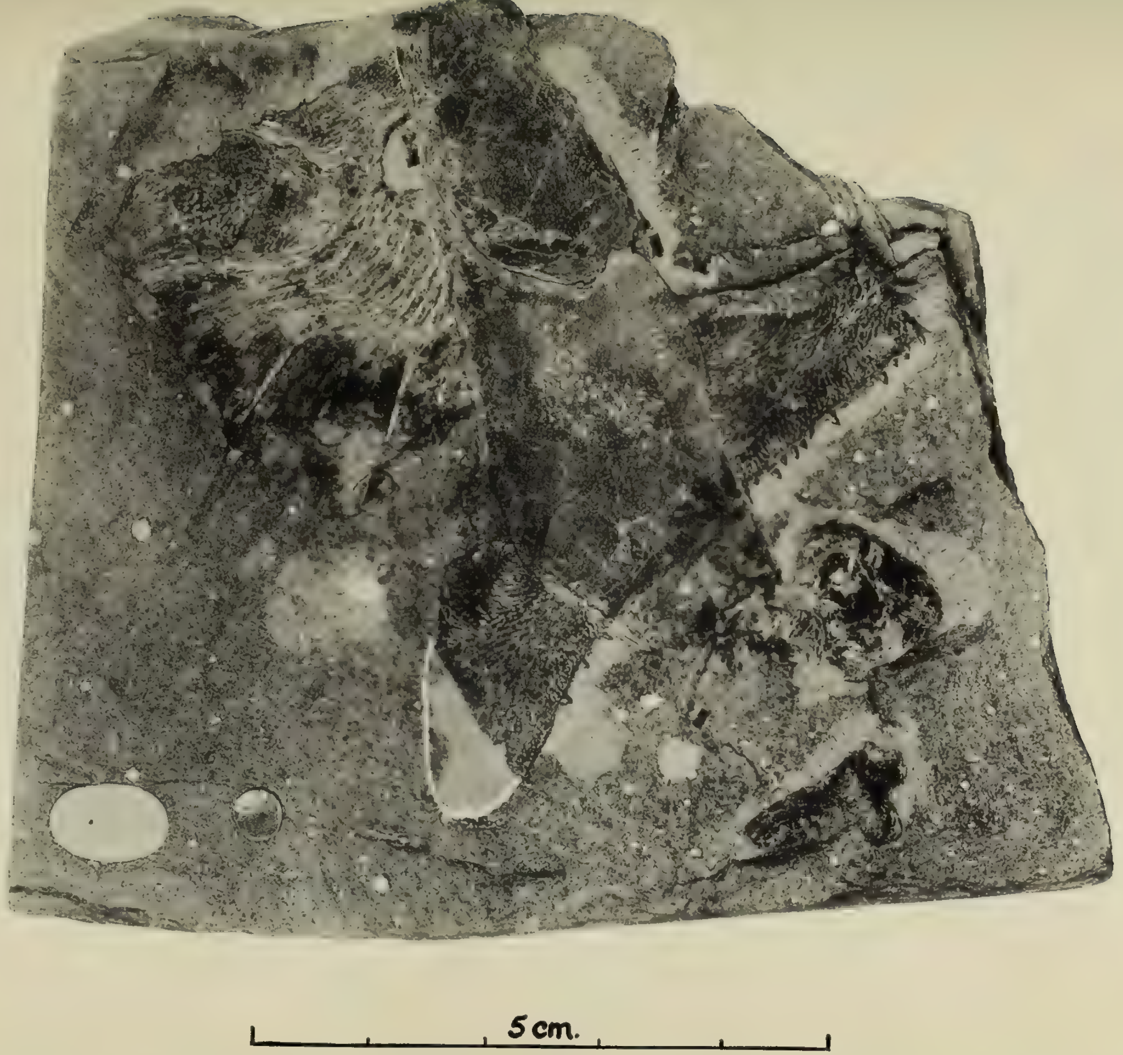

5 cm.

PLATE 38

Ptycholepis monilifer Woodward

Block 3, showing preopercular and dorsal fin. B.M.N.H. 39868.

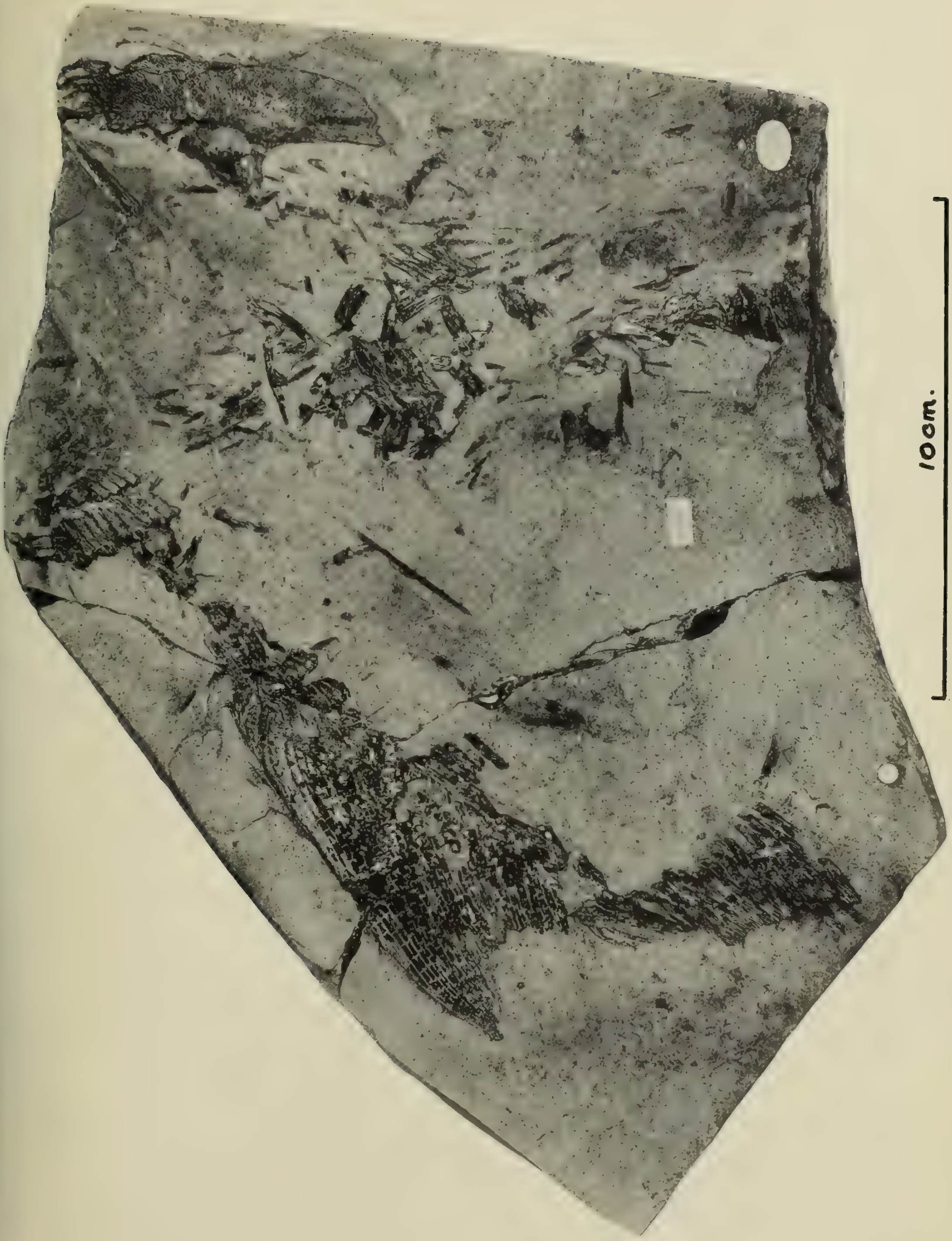

10cm.

PLATE 39

Ptycholepis monilifer Woodward

Block 4, showing tail. B.M.N.H. 39868.

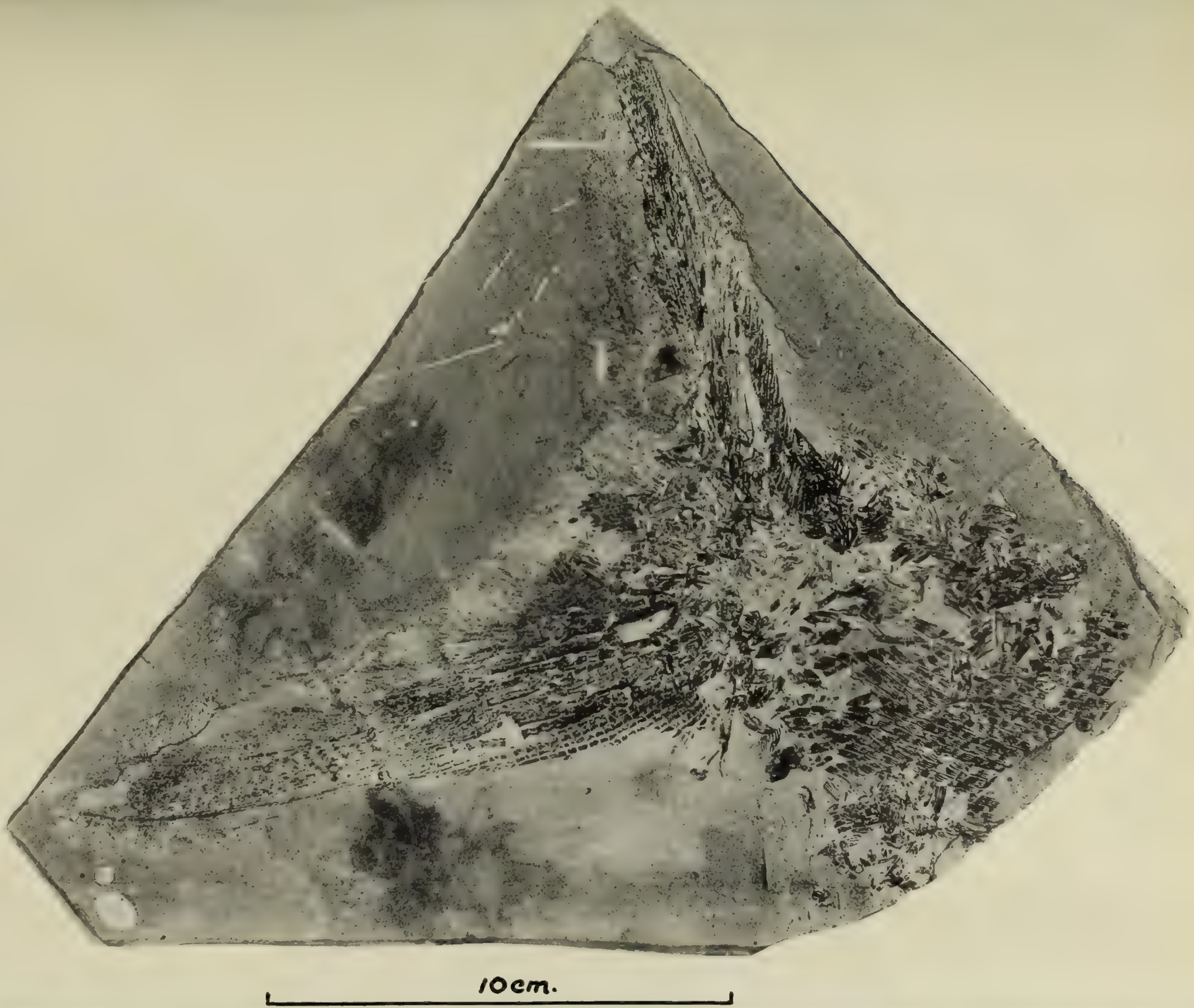

10cm.

PLATE 40

Ptycholepis monilifer Woodward

Block 3, portion of scaling. B.M.N.H. 39868. ×4·1.

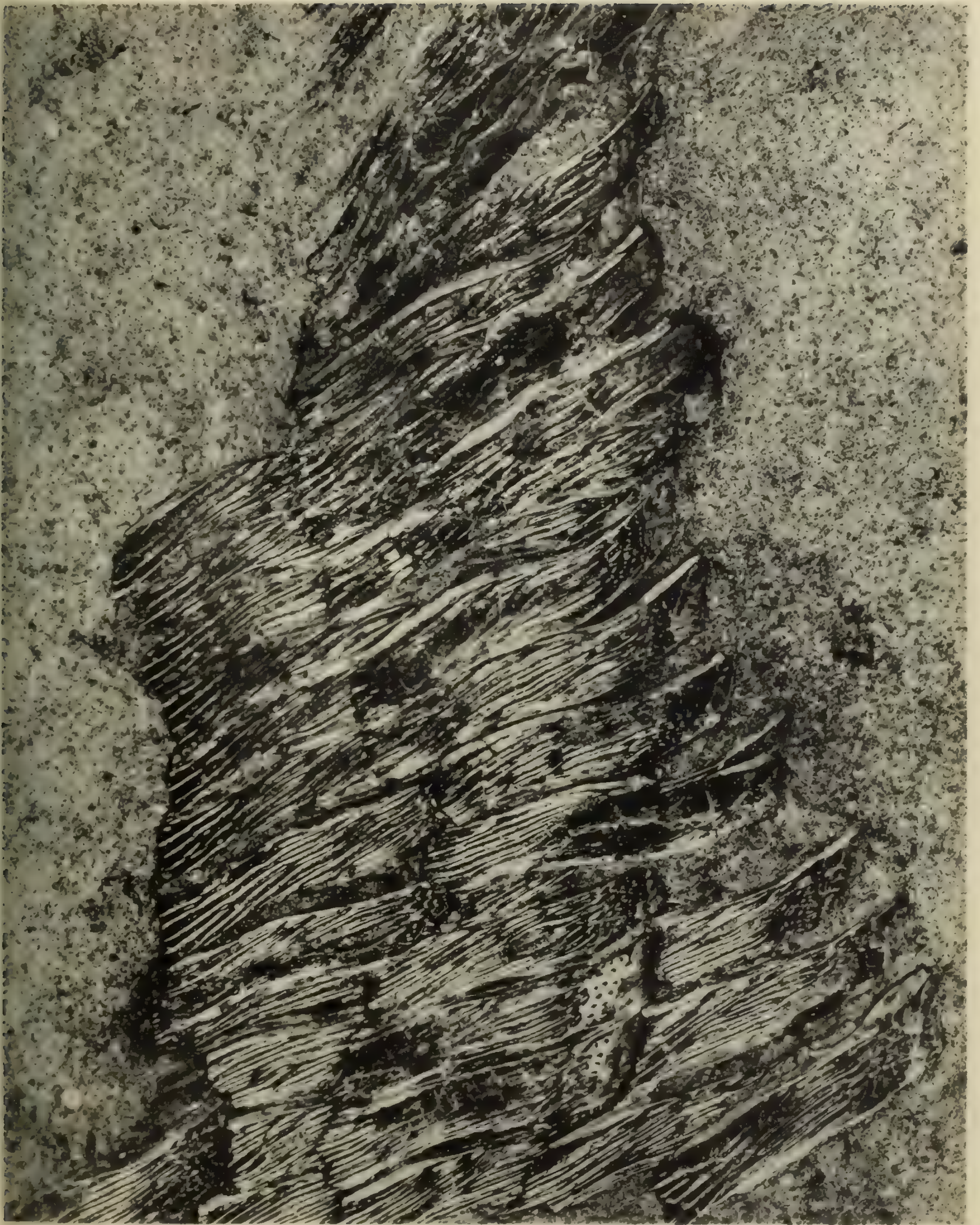
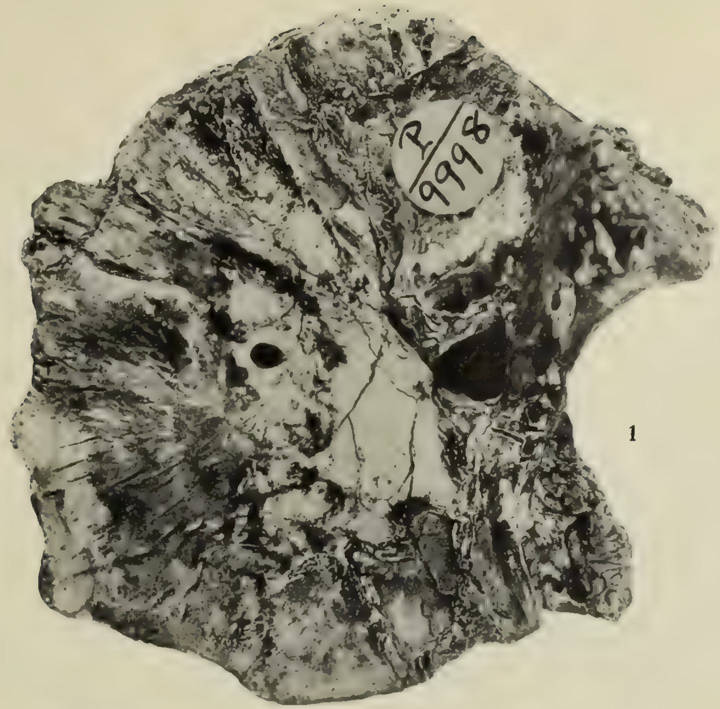


PLATE 41

Lepidotes latifrons Woodward

FIG. 1. Right prootic in lateral view. B.M.N.H. P 9998, scale in mm.

FIG. 2. Stereoscopic photograph of the orbital surface of the right prootic. B.M.N.H. P 9998, scale in mm.



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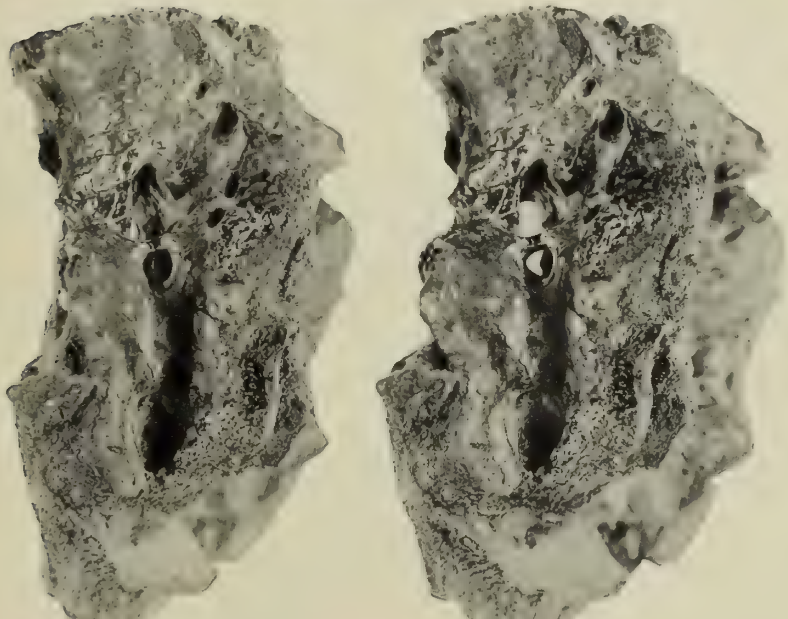


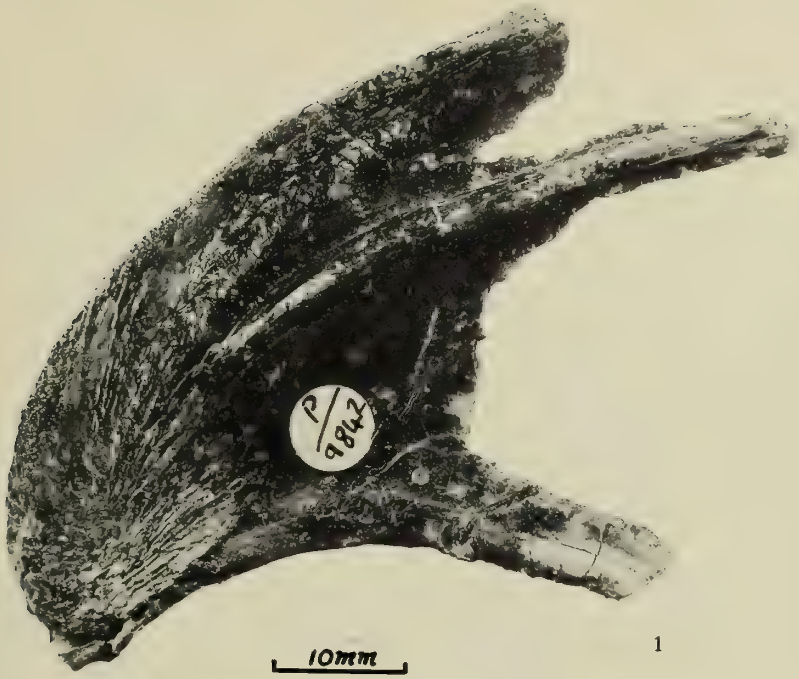
2

PLATE 42

Holophagus gulo Egerton

FIG. 1. Pterygo-quadrate of right side, outer view. B.M.N.H. P 9842, scale in mm.

FIG. 2. Pterygo-quadrate of right side, inner surface. B.M.N.H. P 9842, scale in mm.



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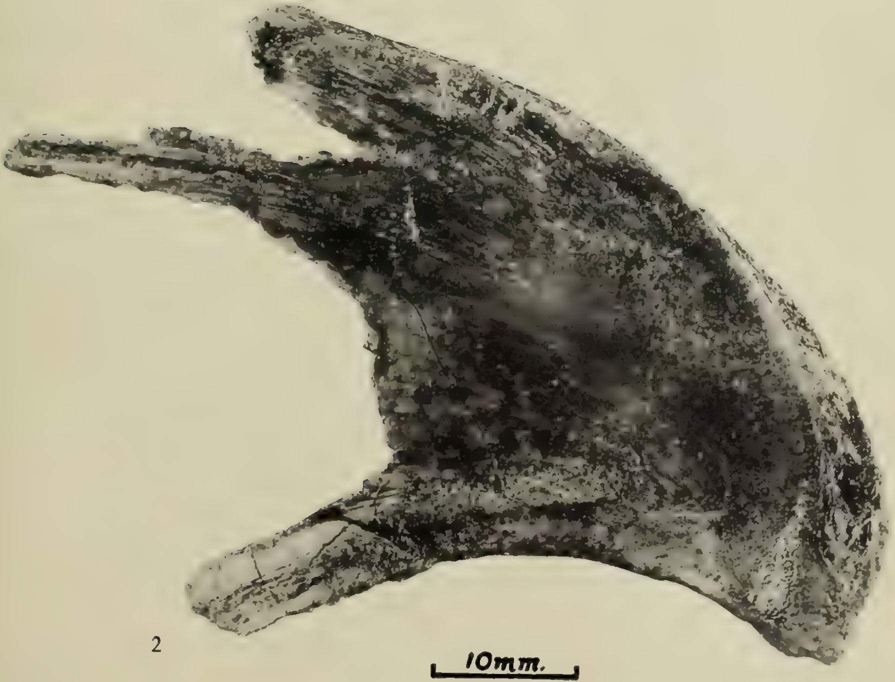


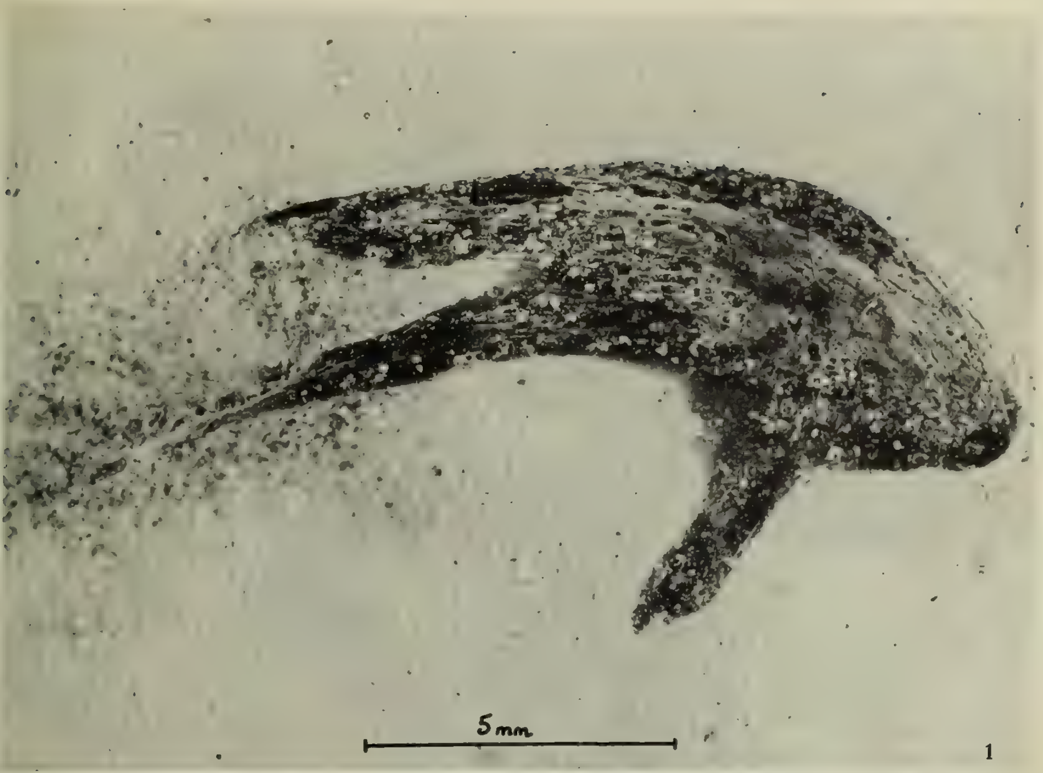
2

PLATE 43

FIG. 1. Pterygo-quadrate of an undetermined Coelacanth. B.M.N.H. P 959.

Holophagus sp.

FIG. 2. Gular plate, ventral view. B.M.N.H. P 4277*a*.



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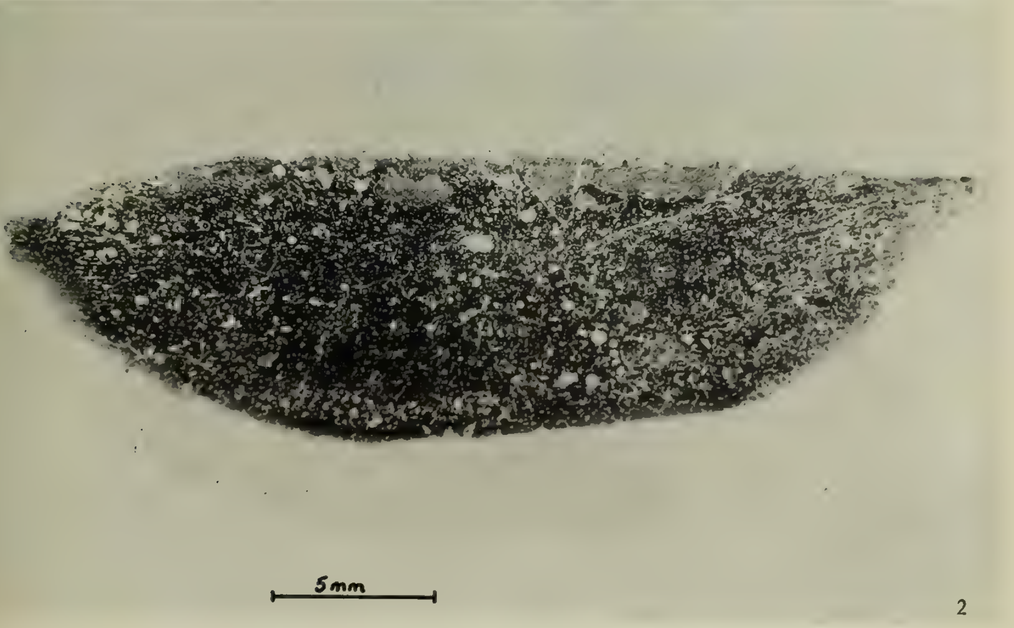

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THE BRITISH CRETACEOUS PLEUROTOMARIIDAE

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L. R. COX

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BY

LESLIE REGINALD COX, F.R.S.

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By L. R. COX

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SYNOPSIS

A study of the British Cretaceous Pleurotomariidae has led to the recognition of at least 49 species, several of which, however, are known only as internal moulds to which it is considered specific names should not be assigned. Of the 40 named species, 28 are new, while 12 have been described by previous authors. Thirty-six of these species are included in the genera *Pleurotomaria, Leptomaria, Bathrotomaria,* and *Conotomaria,* the remainder being described under *Pleurotomaria s. lat.* The species recognized include only 8, records of which from the European continent are thought to be authentic ; many of the others seem to be of very local distribution. Pleurotomariidae are present in almost all British marine Cretaceous formations, and occur in particular variety and abundance in those referable to the Cenomanian stage.

INTRODUCTION

THE only attempts hitherto made to review the British Cretaceous Gastropoda family by family are papers by Tate (1865*a*, *b*) dealing with the " Pterocerae " and " Rostellariae " and by Gardner (1875, 1876, 1877) on the Aporrhaidae, Epitoniidae [Scalidae] and Patellidae. British literature on gastropods of this age is otherwise confined to descriptions of miscellaneous species in such early works as the Sowerbys' *Mineral Conchology* and to a few scattered publications of later date, all except two or three prior to this century. The present paper is a revision of the British Cretaceous Pleurotomariidae, a family well represented in most marine formations of the period, particularly those belonging to the Cenomanian stage. Forty named species are here described, but nevertheless the revision cannot be claimed to approach finality, as several further species, including those of the Cambridge Greensand, are known only by ill-preserved specimens or internal moulds to which reliable identifications cannot be assigned. The most characteristic of the internal moulds, however, are illustrated and reference is made to the names by which they have been recorded in various species lists.

The material studied has been almost confined to the collections of the British Museum (Natural History), the Geological Survey Museum, and the Sedgwick Museum, Cambridge,[1] and I must particularly thank Messrs. S. W. Hester and A. G.

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[1] In the systematic descriptions these are referred to respectively by the abbreviations " B.M." " G.S.M. " and " S.M. "

Brighton, of the second and third of these institutions, for help in the selection of material to borrow for study. Mr. C. W. Wright placed specimens of the family from his own collection at my disposal, and then very kindly presented them to the British Museum (Natural History). Dr. R. Casey, of the Geological Survey, lent me a topotype of *Leptomaria gibsi* which he had collected at Folkestone, and gave valuable assistance in identifying the matrix of various specimens from older collections. Mr. H. G. Owen, of the Department of Palaeontology of the British Museum (Natural History), helped in the same way and showed me several specimens from his own collection. Mr. C. Musgrave, of the Brighton Art Gallery and Museum, searched without success for the holotype of *Pleurotomaria jukesi* Seeley. Mr. W. Smith, of the Chelsea College of Science and Technology, gave helpful advice relating to the recorded locality of the holotype of *Leptomaria hindei*, and Mr. R. L. E. Ford ascertained, by observations in the field, the exact horizons of certain species found at St. Lawrence, Isle of Wight.

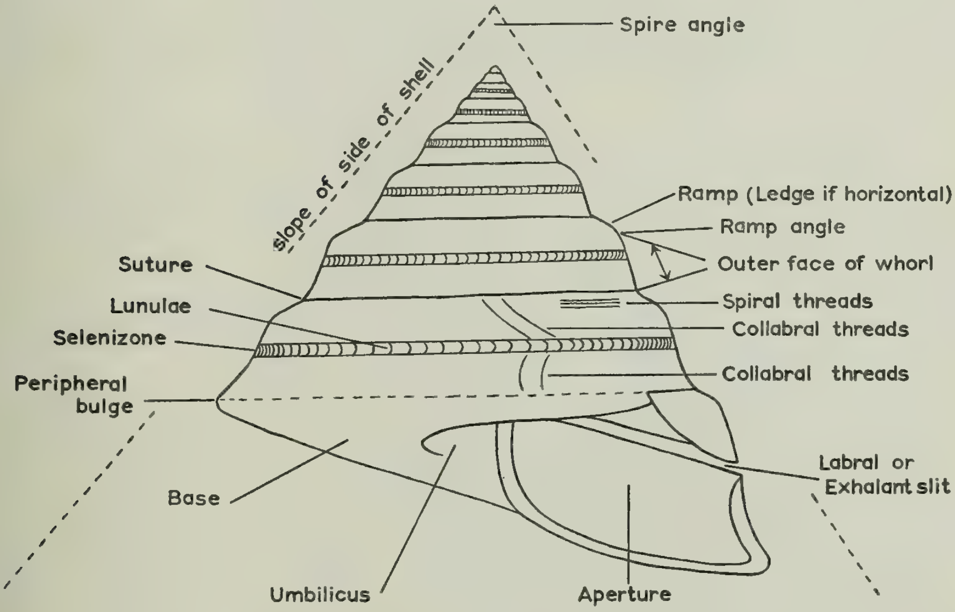
Spire angle
slope of side of shell
Ramp (Ledge if horizontal)
Ramp angle
Outer face of whorl
Suture
Lunulae
Selenizone
Spiral threads
Collabral threads
Collabral threads
Peripheral bulge
Labral or Exhalant slit
Base
Umbilicus
Aperture

FIG. 1. Diagrammatic representation of a species of the family Pleurotomariidae, illustrating descriptive terms here employed.

The descriptive terminology here adopted is largely that introduced by J. Brookes Knight in his various papers on Palaeozoic Pleurotomariacea, as this is to be used in the section of the *Treatise on Invertebrate Palaeontology* dealing with this superfamily. It is explained by the accompanying diagram (Text-fig. 1). Specific discrimination presented no great difficulties. The general character of the ornament, although subject to some variation, was found to be a reliable specific character and to enable such forms as *Bathrotomaria linearis* and *B. dixoni* to be distinguished from *B. perspectiva,* with which they had previously been confused. The position and nature of the selenizone were found to be very constant in the same species. The relative height of the spire is more variable in some forms, and, in the case of *B. perspectiva,* I have come to the same conclusion as previous workers that the very depressed form *B. depressa* must be regarded as one of its synonyms.

The majority of the species described belong to four well-defined groups (*Pleurotomaria, Leptomaria, Bathrotomaria,* and *Conotomaria*), which range up from the Jurassic and to which generic rank has been assigned. Two or three species, however, bear no close resemblance to any others, and are described under *Pleurotomaria sensu lato* rather than under new monotypic genera. Many of the Cretaceous Pleurotomariidae appear to have been of very local distribution and of restricted geological range. Of the species here recognized, only eight can be said definitely to occur on the European continent.

STRATIGRAPHICAL DISTRIBUTION OF SPECIES DESCRIBED

Senonian. The Upper Chalk has yielded *Bathrotomaria regalis* (Roemer) (*Belemnitella mucronata* Zone, Norwich), internal moulds of an indeterminate species, *Pleurotomaria* [*Conotomaria*?] " I " (Upper Senonian, Norwich ; *Micraster cortestudinarium* Zone, Kent) and a number of specimens, mainly internal moulds, which seem referable to *Bathrotomaria perspectiva* (Mantell) (*M. cortestudinarium* and *M. coranguinum* Zones, Kent, Sussex, Wiltshire, Yorkshire).

Turonian. The Chalk Rock, at the base of the *Holaster planus* Zone, has yielded abundant specimens of *Bathrotomaria perspectiva* (Mantell) (Hertfordshire, Bedfordshire, Buckinghamshire, Oxfordshire, Wiltshire, Hampshire). Internal moulds of the same species occur at the same horizon in Kent, Sussex, and elsewhere where the usual Chalk Rock fauna is not present, as well as at lower horizons in the Middle Chalk.

Cenomanian. Holaster subglobosus Zone of Chalk : *Bathrotomaria linearis* (Mantell) (Kent, Surrey), *B. dixoni* sp. nov. (Kent, Isle of Wight, Wiltshire), *B. velata* (Goldfuss) (Kent), *B. regalis* (Roemer) (Kent, Hertfordshire), *Pleurotomaria allobrogensis* Pictet & Roux (Kent).

Schloenbachia varians Zone of Chalk : *Pleurotomaria vectensis* sp. nov. (Kent, Isle of Wight), *P. rockenensis* sp. nov. (Isle of Wight), *Leptomaria hindei* sp. nov. (Wiltshire), *Bathrotomaria linearis* (Mantell) (Kent, Sussex, Isle of Wight, Wiltshire, Somerset), *B. dixoni* sp. nov. (Oxfordshire, Somerset, Dorset), *B. velata* (Goldfuss) (Sussex), *B. ashburneri* sp. nov. (Buckinghamshire, Sussex), *B. perspectiva* (Mantell) (Sussex, Dorset), *B. regalis* (Roemer) (Isle of Wight), *Conotomaria chardstockensis* sp. nov. (Dorset, Wiltshire), *Pleurotomaria* [*Conotomaria*?] "H" (Kent), *Pleurotomaria glyndensis* sp. nov. (Sussex).

Cenomanian Limestone of SE. Devon (not subdivided zonally) : *Leptomaria seatonensis* sp. nov., *L. axmouthensis* sp. nov., *L. wilmingtonensis* sp. nov., *L. hindei* sp. nov. (?), *Bathrotomaria dixoni* sp. nov., *B. velata* (Goldfuss), *Conotomaria percevali* sp. nov., *C. laticarinata* sp. nov., *C. mailleana* (d'Orbigny).

Basal Cenomanian of Warminster, Wiltshire: *Pleurotomaria vectensis* sp. nov., *Leptomaria hindei* sp. nov., *Conotomaria chardstockensis* sp. nov., *C. percevali* sp. nov. (?), *Pleurotomaria* A.

Albian

Upper Albian, *Stoliczkaia dispar* Zone: *Pleurotomaria rockenensis* sp. nov. (Dorset), *P. vectensis* sp. nov. (?) (Isle of Wight), *P. allobrogensis* Pictet & Roux, *Pleurotomaria* " B "–" G " (as internal moulds in Cambridge Greensand).

Gault Clay of Folkestone: *P. plicata* (J. Sowerby) (Lower Upper and Upper Middle Albian, *Hysteroceras orbignyi* Subzone of *H. orbignyi* Zone and *Dipoloceras cristatum* Subzone of *Euhoplites lautus* Zone), *Leptomaria pricei* sp. nov. (horizon unrecorded), *Conotomaria folkestonensis* sp. nov. (horizon unrecorded).

Lower Middle Albian, *Douvilleiceras mammillatum* Zone: *Leptomaria gibsi* (J. Sowerby) (Kent, Bedfordshire).

Lower Albian, *Leymeriella regularis* Subzone of *L. tardefurcata* Zone: *Leptomaria billingtonensis* sp. nov., *Bathrotomaria leightonensis* sp. nov. (both Bedfordshire).

Lower Albian, Shenley Limestone: *P. shenleyensis* sp. nov. *Conotomaria lamplughi* sp. nov.

Aptian

Upper Aptian, Sandgate Beds, *Parahoplites nutfieldensis* Zone: *P. anstedi* Forbes (Surrey).

Upper Aptian, *Parahoplites nutfieldensis* Zone, of Seend, Wiltshire: *Conotomaria seendensis* sp. nov.

Aptian of Upware, near Cambridge: *P. campichei* Keeping.

Aptian, Hythe Beds: *P. toulmini* sp. nov. (probably Kent), *P. anstedi* Forbes (*fide* Dr. R. Casey), *Conotomaria gigantea* (J. de C. Sowerby) (Kent).

Lower Aptian of Isle of Wight: *Bathrotomaria atherfieldensis* sp. nov. (*Deshayesites forbesi* Zone), *Conotomaria gigantea* (J. de C. Sowerby) (*Tropaeum bowerbanki* Zone).

Lower Aptian of Potton, Bedfordshire: *Bathrotomaria ferruginea* (Keeping).

Neocomian

Tealby Limestone (Hauterivian): *Leptomaria donningtonensis* sp. nov., *L. willinghamensis* sp. nov.

Speeton Clay, Bed C4 (Hauterivian): *Pleurotomaria speetonensis* sp. nov. (Very imperfect fragments belonging to two or three other species have been found in the Speeton Clay at various levels.)

Lower Tealby Clay (Hauterivian): *Bathrotomaria nettletonensis* sp. nov.

Claxby Ironstone (Upper Valanginian–Hauterivian): *Bathrotomaria wrighti* sp. nov., *B. swinnertoni* sp. nov.

Spilsby Sandstone (Berriasian): *Pleurotomaria spilsbyensis* sp. nov.

SYSTEMATIC DESCRIPTIONS

Family Pleurotomariidae

Genus *PLEUROTOMARIA* Defrance, 1826

The International Commission on Zoological Nomenclature has recently decided (Opinion 582) that this generic name should be attributed to Defrance notwithstanding its prior but unsatisfactory publication by J. Sowerby in 1821, and also that it should be validated by suppression of the name *Pleurotomarium* de Blainville. 1825.

Type species. *Trochus anglicus* J. Sowerby, 1818, Lias, Europe; designated by S. P. Woodward, 1851.

Generic characters. Trochiform, anomphalous to broadly phaneromphalous, gradate, with outer face of whorls flattened, at least in earlier growth stages. Selenizone at mid-whorl, well below ramp angle when this is present. Ornament of sinuous spiral cords with tubercles at ramp angle and, in some species, at margin of base.

Pleurotomaria toulmini sp. nov.

(Pl. 46, fig. 5)

Material. The holotype only (B.M., G.89481, *ex* Toulmin Smith Coll.), an external mould in hard cherty limestone. The artificial cast illustrated has been prepared from this natural mould and reproduces the external characters of the original shell clearly.

Description. Trochiform, of large-medium size, height (*c.* 55 mm.) approximately equal to diameter, spire angle about 60°. Whorls with inclined, flattened outer face parallel to the general slope of the spire, separated by a well-marked angulation from a gently sloping sutural ramp. Base unknown. Selenizone at middle of whorl outer face, of moderate width, convex, bordered by spiral threads. Two rows of tubercles present, one at ramp angle, the second near lower suture; weak spiral cords are also present on the whole surface, overriding the tubercles.

Remarks. I have hesitated whether to refer this specimen to *Pleurotomaria defrancei* Matheron (1843 : 237, pl. 39, fig. 14), originally described from the Neocomian of Allauch, near Marseilles, and subsequently identified by Pictet & Campiche (1863 : 416, pl. 77, fig. 2) in the Middle Neocomian of Ste Croix (Swiss Jura), and by Peron (1900 : 167, pl. 3, fig. 10) in the Neocomian of Yonne (France). All these records, however, were based on internal moulds, and, while the specimens figured by Pictet & Campiche may well have belonged to the same species as the present one, Matheron's figure represents a specimen in which the outer face of the whorls is vertical and the ramp (at least on the later whorls) is much broader than in this specimen. Only one row of tubercles is shown in Matheron's figure, although a second row is mentioned in his description.

Occurrence. Aptian, Hythe Beds, probably of Kent. The locality of the specimen is unrecorded. Dr. R. Casey informs me its lithology agrees with that of the Hythe Beds as developed at many localities in Kent, and that internal and external moulds of shells occur commonly in this formation, although, being difficult to collect at all complete, they seldom find their way into museum collections.

Pleurotomaria campichei Keeping

(Pl. 48, figs. 1*a–c*, 2)

1883. *Pleurotomaria renevieri* Keeping, p. 98, pl. 4, figs. 1, 1*a* (*non* Pictet & Campiche, 1863).
1883. *Pleurotomaria campichei* Keeping, explan. of pl. 4, figs. 1, 1*a*.

Material. The holotype (S.M., B.19297) and one topotype (G.S.M., 96771).

Description. Small, trochiform, with the height (*c.* 20 mm.) slightly less than the diameter and the spire angle *c.* 80°. Whorls with feebly convex, sloping outer face, rounded shoulder, and narrow sutural ramp; a rather prominent, rounded peripheral bulge is present, broadly crenulated in late growth-stages and not overlapped on spire whorls. Umbilicus narrow, opening gradually into feebly convex base. Selenizone at about mid-whorl, of moderate width, slightly concave, bordered by spiral threads, and with a median spiral thread and strongly arched, closely and regularly spaced lunulae formed by raised threads. Whorl face above selenizone with about three weak spiral threads crossed by well separated, unevenly spaced collabral threads and weak collabral ribs; and between selenizone and peripheral bulge with irregular collabral threads only. Peripheral bulge and base with spiral threads most closely spaced on the bulge and absent from umbilicus; regular transverse threads are well seen in their intervals, and irregular transverse riblets appear at opening of umbilicus and continue on umbilical walls.

Remarks. As the name *P. renevieri*, under which Keeping described this species in his text, was a homonym, the name *P. campichei*, introduced, presumably by an oversight, in the explanation of his plate, is here adopted for the species.

Occurrence. Aptian of Upware, near Cambridge. Keeping stated that the species also occurs at Berklingen, Brunswick, and at Ste Croix, Swiss Jura, but gave no information about the specimens on which these records were based.

Pleurotomaria shenleyensis sp. nov.

(Pl. 48, figs. 6*a–d*)

Material. The holotype only (S.M., B.24566).

Description. Small, trochiform, with the height (14·5 mm.) just exceeding two-thirds of the diameter and the spire angle slightly obtuse. Whorls with feebly convex, sloping outer face, rounded shoulder, and narrow sutural ramp; a rather prominent, rounded peripheral bulge is present, not overlapped on spire whorls. Umbilicus narrow, rather abruptly delimited from feebly convex base. Selenizone at about mid-whorl, of moderate width, flush, bordered by spiral threads, and, where uneroded, with fairly regularly spaced, strongly arched lunulae. Whorl face above selenizone with about three weak spiral cords crossed by weak collabral ribs; and between selenizone and peripheral bulge with about five spiral threads crossed by collabral threads with which they form a regular cancellate pattern. Peripheral bulge and base with spiral threads most closely spaced on the bulge and absent from umbilicus; transverse riblets appear at opening of umbilicus and continue on umbilical walls.

REMARKS. This species closely resembles and was presumably descended from *P. campichei*, from which it differs mainly in its broader spire angle and its wider umbilicus, which merges less gradually into the base.

OCCURRENCE. Lower Albian, Shenley Limestone, Shenley Hill, Bedfordshire.

Pleurotomaria plicata (J. Sowerby)

(Pl. 49, figs. 5, 6*a*, *b*, 7*a–c*)

1816. *Cirrus plicatus* J. Sowerby, p. 94, pl. 141, fig. 3.

MATERIAL. Sowerby's holotype (B.M., 43631), virtually an internal mould; also numerous topotypes (B.M., G.S.M., and S.M.).

DESCRIPTION. Of small-medium size, trochiform, with the height (*c.* 35–40 mm.) usually slightly less than the diameter and the spire angle 90° or rather less. Whorls with steep, obtusely angular outer face, a rounded shoulder, and a narrow sutural ramp; a slight peripheral bulge is present, crenulated in some specimens and not overlapped on spire whorls. Umbilicus narrow, base moderately convex. Selenizone at a mid-whorl angulation, narrow, flush, bordered by spiral threads, with feebly arched to almost straight, prosocline lunulae formed by raised threads, and in some specimens with about two weak spiral threads. Whorl face above selenizone with ten or more unevenly spaced spiral threads or cords, crossed by uneven collabral threads and, on the ramp, by broad collabral ribs; and between selenizone and peripheral bulge with eight to ten spiral threads, crossed by irregular collabral threads forming a cancellate pattern in places. Peripheral bulge and base with spiral threads and cords, with intervals that are broadest, on the average, adaxially; transverse threads are weak and riblets absent on the base.

OCCURRENCE. Gault Clay of Folkestone, Kent, abundant in Price's Bed 8 (Upper Middle Albian, *Dipoloceras cristatum* Subzone of *Euhoplites lautus* Zone), rare in Bed 9 (Lower Upper Albian, *Hysteroceras orbignyi* Subzone of *H. orbignyi* Zone).

Pleurotomaria vectensis sp. nov.

(Pl. 50, figs. 8, 9, 10*a–c*)

MATERIAL. The holotype (B.M., G.3421) and one paratype (S.M., B.34838), the former retaining much and the latter a little of the shell; also numerous internal moulds thought to belong to the same species.

DESCRIPTION. Of small-medium to medium size (diameter of holotype, 28·5 mm.; of largest internal mould, 58 mm.), depressed-conical, with spire angle about 40°. Whorls with almost flat outer face, sloping to conform with the general slope of the spire, a rounded shoulder, and narrow sutural ledge. Periphery sharply angular, base flattened and impressed. Selenizone relatively wide, almost flush, at about mid-whorl well below the shoulder, bordered by spiral threads, and bearing a median spiral thread, very faint spiral striae, and rather distant, irregularly spaced, strongly arched, thread-like lunulae. Whorl face above selenizone with three spiral cords occupying the shoulder and sutural ledge, where they override transversely elongated tubercles; and between selenizone and periphery with four spiral cords crossed, on earlier whorls, by collabral threads which form a cancellate pattern with them and produce small nodes at the points of intersection. Base with irregularly spaced spiral threads which enter umbilicus and are most closely arranged near the periphery, but without transverse ornament.

Remarks. An imperfect specimen (B.M., G.81302) from the Upper Greensand (Upper Albian) of St. Lawrence, collected by Mr. R. L. E. Ford, differs from the holotype in the presence of transverse riblets at the umbilical opening and in the fewer spiral cords on its base. It may prove to belong to a distinct although related species.

Occurrence. A possible representative in the Upper Albian, Upper Greensand, of St. Lawrence, Isle of Wight. Lower Cenomanian, *Schloenbachia varians* Zone, Glauconitic Marl, of Sand Rock Spring, near Chale (type locality), Compton Bay, St. Catherine's Point, and St. Lawrence, all Isle of Wight. Lower Cenomanian of Warminster, Wiltshire. Cenomanian (Lower Chalk) of Lewes and Eastbourne, Sussex, and of Folkestone, Kent.

Pleurotomaria rockenensis sp. nov.

(Pl. 51, figs. 2*a*–*c*, 3, 4*a*, *b*)

Material. The holotype (B.M., G.89490, C. W. Wright Coll.), two paratypes retaining portions of their shell, and several internal moulds assumed to belong to the same species.

Description. Of small-medium size, very depressed, with the diameter (*c.* 40 mm. in the largest specimen) well exceeding twice the height and the spire angle 110° or more, the proportions varying to some extent. Whorls with a sloping, almost flat outer face, a well-marked shoulder, and a subhorizontal sutural shelf; a rounded peripheral bulge is present. Base feebly convex and low, the aperture being very broad in proportion to its height. Umbilicus relatively narrow. Selenizone below whorl shoulder, moderately wide, almost flush, bordered on each side by a spiral thread, and bearing faint spiral striae and weak, well-arched, thread-like lunulae. Ornament consisting of a row of conspicuous rounded tubercles on the sutural shelf, two faintly nodose spiral threads between the selenizone and peripheral bulge, small transversely elongated nodes crossed by spiral cords on the peripheral bulge, and numerous unequal spiral cords, some obscurely nodose, on the base.

Remarks. This may be the species recorded (Jukes-Browne & Hill, 1904 : 473) as *P. moreausiana* d'Orbigny, the original figures of which (d'Orbigny, 1843, pl. 199, figs. 3–6) represent, however, a shell with a very sharply carinate periphery.

Occurrence. Lower Cenomanian (Glauconitic Marl) of Rocken End (type locality), St. Catherine's Point, Sand Rock Spring, near Chale, and Ventnor; all Isle of Wight. Uppermost Albian (*Stoliczkaia dispar* Zone), Holworth House cliffs, South Dorset.

Genus ***LEPTOMARIA*** E. Eudes-Deslongchamps, 1864

Type species. *Pleurotomaria amoena* J. A. Eudes-Deslongchamps, Bajocian, France; by original designation.

Generic characters. Conical or cyrtoconoid, anomphalous to broadly phaneromphalous; whorls weakly to strongly convex, not angular, the last rounded at periphery of convex base; selenizone at mid-whorl; ornament of spiral threads cancellated in some species by collabral threads.

Leptomaria donningtonensis sp. nov.

(Pl. 46, figs. 3, 4)

Material. The holotype (S.M., B.11676); a second specimen (S.M., B.11677) is considered to be a crushed representative of the species.

Description. Of medium size, turbiniform, the diameter (43 mm.) slightly exceeding the height in the holotype; if, however, the almost planispiral coiling of the early whorls and consequent apical truncation are due to compression, the original height must have been approximately equal to the diameter. Whorls strongly convex, the last evenly rounded at margin of moderately convex base. No umbilicus. Selenizone at or slightly above mid-whorl, rather broad, convex, with well-separated, prominent lunulae (seen in B.11677). Whorl face bearing above selenizone four to five spiral cords crossed by weak collabral riblets, and between selenizone and lower suture about five nodose spiral cords; base with numerous spiral cords with narrow intervals.

Occurrence. Hauterivian, Tealby Limestone, Donnington, Lincolnshire (type-locality). The specimen B.11677 is from the same formation at North Willingham, Lincolnshire.

Leptomaria willinghamensis sp. nov.

(Pl. 46, figs. *7a, b*)

Material. The holotype only (S.M., B.11675).

Description. Of small-medium size, trochiform, with the height (originally *c.* 22 mm.) slightly less than the diameter and the spire angle approximately a right angle. Whorls with a narrow sutural shelf, below which they are feebly and evenly convex; periphery sharply carinate. No umbilicus. Selenizone a rather narrow projecting cord just below mid-whorl. Whorl face both above and below selenizone bearing fine collabral riblets forming a cancellate pattern with weaker, narrow, rather numerous spiral cords. Ornament of base unknown.

Remarks. The ornament is coarser than in *L. billingtonensis* and there is no umbilicus.

Occurrence. Hauterivian, Tealby Limestone, North Willingham, Lincolnshire.

Leptomaria billingtonensis sp. nov.

(Pl. 48, figs. *7a–d*)

Material. The holotype (B.M., G.65274) and one paratype (G.61263).

Description. Of small-medium size, turbiniform, diameter (*c.* 25 mm.) very slightly exceeding height ; spire angle slightly less than a right angle. Whorls evenly and rather strongly convex, periphery broadly rounded. Base convex, with narrow umbilicus. Selenizone at mid-whorl, narrow, flat, almost flush, bordered on each side by a faint spiral groove and bearing close-spaced, feebly arched lunulae and obscure spiral threads. Whorl face, both above and below selenizone, ornamented with numerous spiral and collabral threads, forming a cancellate pattern. Ornament of base imperfectly known, apparently of a similar type.

Remarks. The actual surface of the shell, showing the ornament, is preserved only on small portions of the holotype. Otherwise, the specimens retain at the most only the inner layers of the shell. Its greater height readily distinguishes this species from *L. gibsi* and *L. pricei*.

Occurrence. Lower Albian, *Leymeriella regularis* Subzone of *L. tardefurcata* Zone, Arnold's (formerly Pratt's) Pit, Billington Crossing, near Leighton Buzzard, Bedfordshire.

Leptomaria gibsi (J. Sowerby)

(Pl. 49, figs. 1, 2*a*, *b*, 3)

1821. *Trochus gibsi* J. Sowerby, p. 139, pl. 278, fig. 1.
1843. ? *Pleurotomaria gurgitis* (Brongn.) : d'Orbigny, p. 249, pl. 192, figs. 4–6 (*non* Brongniart sp.).

Material. Holotype (B.M., 43630). Topotypes, similarly preserved, in the same and in the Geological Survey Museums (R. Casey Coll.). Several specimens from other localities, as stated below.

Description. Of small-medium size, trochiform, with height (*c.* 17 mm. in the holotype) about four-fifths of the diameter and the spire angle slightly exceeding 90°. Whorls feebly and evenly convex, the last subcarinate at periphery. Base feebly convex, with narrow umbilicus. Selenizone moderately wide, at mid-whorl, flush, between narrow spiral grooves and with a narrow median groove. Whorl face, above and below selenizone, with fine spiral and collabral threads forming a delicate cancellate pattern ; ornament of base unknown.

Remarks. The holotype (Pl. 49, figs. 2*a*, *b*) is a phosphatized specimen in which the outer shell layer has disappeared, leaving an inner layer which is smooth except for faint spiral striations and growth-lines best seen on the base. Dr. R. Casey has collected topotypes which are similarly preserved except that in one (Pl. 49, fig. 3) a small area of the original surface remains and shows the delicate cancellate ornament described above. An impression of the ornament of most of the upper surface of the shell (Pl. 49, fig. 1) is preserved on an external mould (B.M., G.55140) from near Leighton Buzzard, and a specimen from Borough Green (G.S.M., Zm 1075) retains a small patch of shell showing the selenizone and surface ornament, which agree well with the impression preserved on the external mould just mentioned.

The French Albian specimens figured by d'Orbigny (1843) as *Pleurotomaria gurgitis* may have belonged to *L. gibsi* and are quite distinct from the taller form to which the name *Trochus gurgitis* was originally given by Brongniart, and which Pictet & Roux (1849 : 223) thought might be Sowerby's *Solarium conoideum*. A shell from the Cenomanian of Syria figured as *L. gibbsi* by Delpey (1939 : 61, text-figs. 37, 38) differs in the distinct median angulation of its whorls.

Occurrence. Lower Middle Albian, Lower Gault, main *Douvilleiceras mammillatum* Zone, of Folkestone (type locality) ; *D. mammillatum* Zone of Borough Green, Wrotham, and Bearsted, Kent, and of Gatehouse Pit, Grovebury, Leighton Buzzard, Bedfordshire.

Leptomaria pricei sp. nov.

(Pl. 49, figs. 8*a–c*)

Specific name. Named after F. G. H. Price, who in 1874 described the Gault succession at Folkestone.

Material. The holotype (S.M., B.31837) ; also several paratypes (mostly B.M.).

Description. Of small-medium size, low-turbiniform, with the diameter (36 mm. in the holotype) four-thirds of the height and the spire angle about 120°. Whorls strongly and evenly convex, their surface curving round to become horizontal where it meets the suture ; last whorl carinate at periphery. Base rather strongly convex ; umbilicus moderately wide. Selenizone a narrow, smooth, strongly convex cord at mid-whorl. Whorl face, both above and below selenizone, with narrow, unequal, closely spaced spiral threads and cords which bear small nodes where crossed by somewhat irregular, weak collabral threads ; on the last whorl of the holotype there are about ten spirals above the selenizone and eighteen below it. Base with numerous more or less nodose spiral cords which are most closely spaced near the periphery.

Remarks. The much stronger convexity of the whorls and the narrow selenizone readily distinguish this species from *Leptomaria gibsi*. The less distinctly shouldered whorls, the absence of definite ribs near the suture, and the narrowness and prominence of the selenizone distinguish it from *Pleurotomaria plicata*, which occurs in a similar matrix of Gault Clay.

Occurrence. Albian, Gault Clay (exact bed unrecorded), Folkestone, Kent.

Leptomaria seatonensis sp. nov.

(Pl. 54, figs. 1*a*, *b*, 2)

Material. The holotype (B.M., G.89493, C. W. Wright Coll.) ; also two paratypes (B.M.).

Description. Of medium size (diameter of largest specimen 47 mm.), broadly conical, the diameter only slightly exceeding the height. Whorls strongly and evenly convex. Base convex ; umbilicus of moderate width. Selenizone at mid-whorl, broad, flush, smooth or with faint spiral grooves crossed by the faint lunulae. Whorl face ornamented with numerous unequal spiral threads crossed near the upper suture, most conspicuously on the earlier whorls, by weak collabral riblets. Base with unevenly spaced concentric grooves.

REMARKS. *Leptomaria royana* (d'Orbigny), Cenomanian of France, is the most closely comparable species of approximately the same geological age described from other areas, but the details of its ornament are unknown.

OCCURRENCE. Cenomanian Limestone of Havencliff, ¾ mile E. of Seaton, Devon (Bed B of Jukes-Browne).

Leptomaria axmouthensis sp. nov.

(Pl. 52, figs. 4*a*, *b*, 5*a*, *b*)

MATERIAL. The holotype (S.M., B.34824) and one paratype (S.M.).

DESCRIPTION. Of medium size (diameter of larger specimen 46 mm.), low-turbiniform, with obtuse, cyrtoconoid spire and strongly and evenly convex whorls abutting simply at the sutures. Height of aperture slightly less than that of spire. No peripheral bulge. Base strongly convex ; umbilicus wide. Selenizone slightly above mid-whorl, narrow, flat, with closely and unevenly spaced lunulae. Whorl face with rather unevenly arranged spiral threads and cords, rendered obscurely granose, particularly on the earlier whorls, by closely spaced collabral threads. Similar ornament occupies the outer part of the base, but is replaced towards the umbilicus by flat bands varying in width.

REMARKS. The relatively higher spire, the broader umbilicus, and the absence of a peripheral bulge distinguish this species from *Leptomaria hindei*.

OCCURRENCE. Cenomanian Limestone of Axmouth, E. of Seaton, Devon (Beds 11 and 12 of Mayer).

Leptomaria wilmingtonensis sp. nov.

(Pl. 51, figs. 5, 6*a*, *b*)

MATERIAL. The holotype (B.M., G. 89495) and two paratypes (B.M.).

DESCRIPTION. Of medium size (diameter of largest specimen 44 mm.), depressed-conical, with obtuse, slightly cyrtoconoid spire and flat to feebly convex whorls separated by narrowly channelled sutures. Height of aperture about one-half of that of spire. A slight peripheral bulge, not completely overlapped on the spire whorls, is present. Base feebly convex ; umbilicus very narrow. Selenizone broad, flush, at mid-whorl. Face of whorls ornamented with unequal spiral cords (largely obliterated by erosion in the available specimens), and, near the upper suture, with transversely elongated tubercles which apparently die out on the last whorl. Base smooth except for growth-rugae and (in one specimen) obscure spiral threads around the umbilicus.

REMARKS. The very narrow umbilicus and the flatter whorls readily distinguish this species from *L. axmouthensis* and *L. hindei*.

OCCURRENCE. Cenomanian Limestone of Wilmington, near Honiton, Devon.

Leptomaria hindei sp. nov.

(Pl. 51, figs. 1*a–c*)

MATERIAL. The holotype (B.M., G.27577, G. J. Hinde Coll.) and two paratypes (G.S.M., 96767–8).

DESCRIPTION. Medium-sized (diameter of largest specimen *c.* 70 mm.), low-turbiniform, with obtuse, cyrtoconoid, dome-like spire and strongly and evenly convex whorls separated by a channelled suture. Last whorl relatively high, with a very slight, angular peripheral bulge. Base strongly convex, umbilicus moderately wide. Selenizone at mid-whorl, details of its structure unknown. Whorl face with numerous narrow, slightly unequal spiral threads and cords. Similar ornament occupies the outer part of the base, but is replaced towards the umbilicus by more distant, shallow spiral grooves. Transverse ornament almost confined to broad, coarse rugae at umbilical margin.

REMARKS. Two specimens from Devizes seem to be those recorded in the Lower and Middle Chalk Memoir (Jukes-Browne & Hill, 1903 : 163) as *Pleurotomaria brongniartiana* d'Orbigny, but they differ from that species, as figured by d'Orbigny (1843, pl. 203, figs. 1–4) in their more dome-like spire and less angular periphery. They are, perhaps, more closely comparable to that author's (1843, pl. 203, figs. 5, 6) *P. royana*, founded, however, on an internal mould.

OCCURRENCE. Cenomanian, probably of South Devon, and of Devizes, Wiltshire. (The locality of the holotype was recorded as " Shalford " on the collector's original label, retained with the specimen, but could not have been Shalford, near Guildford, so that it seems possible that the label was misplaced. The matrix is exactly like that of specimens from the Cenomanian Limestone of Devon.) A somewhat doubtful specimen (S.M.) is from the Cenomanian of Warminster, Wiltshire.

Genus ***BATHROTOMARIA*** Cox, 1956

TYPE SPECIES. *Trochus reticulatus* J. Sowerby, Upper Jurassic ; by original designation.

GENERIC CHARACTERS. Trochiform, elevated to depressed, anomphalous to broadly phaneromphalous ; whorls (at least in earlier growth-stages) angulate, with usually broad ramp ; a second carina or angulation, just overlapped on spire, delimiting base ; selenizone at ramp angle ; ornament of spiral threads commonly cancellated by collabral threads.

Bathrotomaria wrighti sp. nov.

(Pl. 45, figs. 4*a–d*)

MATERIAL. The holotype only (B.M., G.89484, C. W. Wright Coll.).

DESCRIPTION. Of medium size, depressed-trochiform, with the diameter (50 mm.) well exceeding the height (32 mm.). Whorls obtusely angular, with the ramp gently sloping and feebly convex, and about equal in width to the moderately steep whorl outer face. A slight peripheral bulge is present. Base of moderate convexity; umbilicus broad. Details of selenizone unobservable. Whorl face ornamented everywhere with moderately strong spiral threads and bearing narrow collabral riblets on the part of the ramp near the suture. Base unornamented, umbilical walls with narrow transverse riblets.

REMARKS. No closely comparable species of Lower Cretaceous age has been described previously. *B. linearis* (Mantell), from the Cenomanian, has more numerous and finer spiral threads.

OCCURRENCE. Neocomian, Hauterivian, Claxby Ironstone, Nettleton Top Mine, Lincolnshire.

Bathrotomaria swinnertoni sp. nov.

(Pl. 45, figs. 2*a*, *b*, 3)

SPECIFIC NAME. Named after Professor H. H. Swinnerton in recognition of his work on English Neocomian palaeontology.

MATERIAL. The holotype (B.M., G.89485) and one paratype (G.89486), both C. W. Wright Coll.

DESCRIPTION. Small, trochiform, with the height (10 mm. in the paratype) slightly less than the diameter (11·2 mm.) and the spire angle slightly less than 90°. Whorls obtusely angular, with the outer face flat and sloping and the ramp broad, flat, and inclined to the horizontal at an angle of about 45°. Periphery rounded, bulging slightly in places. Base feebly convex; no umbilicus. Selenizone a projecting cord of moderate width at ramp angle, bearing equidistant, slightly arched, filiform or even stronger lunulae. Entire surface, including base, ornamented with spiral threads of unequal strength with broader intervals, and with evenly spaced growth-threads, forming a delicate cancellate pattern; there are about five to eight spirals on the ramp and seven on the whorl outer face.

OCCURRENCE. Neocomian, Hauterivian, Claxby Ironstone, Nettleton Top Mine, Lincolnshire.

Bathrotomaria nettletonensis sp. nov.

(Pl. 46, figs. 1*a*–*c*)

MATERIAL. The holotype only (B.M., G.89487, C. W. Wright Coll.).

DESCRIPTION. Of medium size, depressed-turbiniform, with the height (27 mm.) about three-fifths of the diameter, and a dome-like spire. Whorls with a feebly convex, rather steeply sloping outer face and a broad, feebly convex, very gently inclined ramp. Periphery broadly convex, without bulge. Base rather strongly convex, umbilicus wide. Selenizone at ramp angle, moderately wide, strongly convex, the details of its ornament not preserved. Ramp, whorl outer face and outer part of base bearing spiral cords of unequal width; these are crossed, on peripheral region only, by weak collabral riblets. Remainder of base smooth.

REMARKS. This species is distinguished from *B. wrighti* by its more depressed spire, the strongly convex selenizone, and the coarser spiral ornament. It is not a very typical *Bathrotomaria*, but agrees better with that genus than with *Leptomaria*.

OCCURRENCE. Neocomian, Hauterivian, Lower Tealby Clay, Nettleton Top Mine, Lincolnshire.

Bathrotomaria speetonensis sp. nov.

(Pl. 45, figs. 5, 6*a*, *b*)

1878. *Trochus complicatus* Forbes MS. : E. T. Newton, p. 22 (*nom. nud.*).

MATERIAL. The holotype (B.M., G.55232) and two paratypes (G.S.M., 96772–3).

DESCRIPTION. Of small-medium size (diameter *c.* 38 mm.), trochiform, height probably about equal to diameter (early whorls are missing in available specimens). Whorls with a flat or feebly convex, steep outer face, separated by a well-marked angulation from a broad, very gently sloping, feebly convex sutural ramp. Periphery angular, base flattened-convex, no umbilicus. Selenizone of moderate width, strongly convex, at ramp angle. Ramp ornamented with twelve or more weak spiral threads and with weak collabral threads confined to the neighbourhood of the suture; outer face of whorls with up to about twelve spiral threads or cords, which are weakest and most closely spaced near the selenizone and are crossed by collabral rugae.

OCCURRENCE. Neocomian, Hauterivian, Bed C4, Speeton, Yorkshire.

Bathrotomaria atherfieldensis sp. nov.

(Pl. 46, figs. 2*a*, *b*)

MATERIAL. The holotype only (B.M., G.432).

DESCRIPTION. Small, trochiform, diameter (*c.* 26 mm.) slightly exceeding height, spire angle about 90°. Whorls obtusely angular, with steep outer face and broad ramp forming an angle of 30°–40° with the horizontal. Periphery rounded, base feebly convex; no umbilicus. Selenizone a moderately broad, strongly convex, almost smooth cord at ramp angle. Ramp and whorl outer face bearing rounded spiral cords with linear intervals, subordinate collabral rugae, and close-spaced collabral threads visible in places in the intervals; there are about nine spiral cords on the ramp and seven on the outer face. Base ornamented with rounded spiral cords near periphery and with broader, flat bands of unequal width on its inner part, together with subordinate transverse threads and rugae, as on whorl face.

OCCURRENCE. Lower Aptian, *Deshayesites forbesi* Zone, Lower Lobster Bed (top of Atherfield Clay), Atherfield, Isle of Wight.

Bathrotomaria ferruginea (Keeping)

Pl. 46, fig. 6

1883. *Pleurotomaria ferruginea* Keeping, p. 99, pl. 4, figs. 2*a*, *b*.

MATERIAL. The holotype (S.M., B.19304) and one topotype (B.M., 66365).

DESCRIPTION. Moderately large, conical, diameter (up to 93 mm.) slightly less than height, spire angle about 60°. Whorls very obtusely angular, the last with a slight bulge at its subangular periphery. Base rather flattened, umbilicus very narrow. Selenizone, at whorl angulation, a very narrow, smooth cord between two linear grooves. Whorl face ornamented with numerous unequal and unevenly spaced linear grooves, with subordinate growth-rugae and, in places only, collabral threads forming a cancellate pattern with the spirals. Base unornamented except near the periphery, where faint, close-spaced linear grooves occur.

OCCURRENCE. Lower Aptian, Potton, Bedfordshire.

Bathrotomaria leightonensis sp. nov.

(Pl. 48, figs. 3*a*, *b*, 4)

MATERIAL. The holotype (B.M., G.89488) and one paratype, an external mould (G.89489), both C. W. Wright Coll. Three specimens in the Sedgwick Museum (B.58436–8), internal moulds or virtually so, probably belong to this species.

DESCRIPTION. Of small-medium size, depressed-trochiform, height (*c.* 17 mm. in the holotype) three-quarters of the diameter or more; spire angle from about 90°–110°. Whorls obtusely angular, with steep, almost vertical outer face and a broad, flattened ramp inclined to the horizontal at an angle of about 40°; periphery with a slight subangular bulge. Base feebly convex, umbilicus probably absent. Selenizone, at ramp angle, of moderate width, flush, bearing three longitudinal threads and well-arched, thread-like lunulae. Surface, including base, ornamented with spiral threads crossed by fairly evenly and closely spaced collabral threads, forming a cancellate pattern; the spiral threads number about nine on the ramp and eight on the outer face, and they are closely arranged on the base.

REMARKS. In this species the spiral ornament is more delicate and the collabral threads are better developed than in *B. atherfieldensis*.

OCCURRENCE. Lower Albian, *Leymeriella regularis* Subzone, Arnold's Pit, Billington Crossing, near Leighton Buzzard, Bedfordshire.

Bathrotomaria linearis (Mantell)

(Pl. 55, figs. 3*a–c*, 4)

1822. *Trochus linearis* Mantell, p 110, pl. 18, figs. 16, 17.
1840. *Trochus linearis* Mant.: Geinitz, p. 46, pl. 13, figs. 6 (?), 8*a*, *b*; pl. 15, figs. 18 (?), 19 (?).
1889. *Pleurotomaria linearis* Mant.: Fritsch, p. 74, text-fig. 48.
1898. *Pleurotomaria plana* Münst.: Müller, p. 85, pl. 12, figs. 3, 4 (*non* Münster).

MATERIAL. Mantell's two syntypes (B.M. 8628, 8639), the second of which (8639, Mantell's fig. 17, Pl. 55, figs. 3*a–c* of the present paper) is selected as lectotype. Also numerous other specimens, some doubtfully identified owing to imperfect preservation.

DESCRIPTION. Of medium to large-medium size (diameter of largest specimens *c.* 100 mm.), depressed-conical, with the diameter about twice the height and the spire angle about 100° in the lectotype. Whorls very obtusely angular, with sloping outer face and well inclined ramp which is as wide as the outer face or even slightly wider. Last whorl subangular and with a slight bulge at periphery. Base flattened-convex, umbilicus moderately broad. Selenizone a smooth, convex cord of moderate width at whorl angulation. Ornament of outer face and ramp consisting of spiral threads or cords, of which those on the ramp are obscurely nodose or cancellated by fine collabral threads in early growth stages. Base with concentric riblets and threads which mostly alternate in strength.

Remarks. Unfortunately all the available specimens, including the syntypes, are indifferently preserved, but the distinctive characters of the species are easily recognizable. The subangular periphery with its slight bulge distinguishes *B. linearis* from full-grown specimens of *B. perspectiva*, the broader ramp, narrower selenizone, and absence of transverse riblets from *B. dixoni*. I refer to *B. linearis* the specimen from the Lower Senonian of Germany figured by Müller as *Pleurotomaria plana*, but the true Upper Senonian *P. plana*, which Holzapfel (1888, pl. 20, figs. 5*a*, *b*) has figured, is more depressed, with rounded rather than angular whorls.

Occurrence. Cenomanian, *Schloenbachia varians* Zone, of Hamsey, near Lewes, Sussex (type locality) and of various localities in Kent, Sussex, the Isle of Wight, Wiltshire and Somerset. It would appear from the references to Fritsch and Müller cited above that on the European continent the range of the species extends up into the Turonian and Lower Senonian.

Bathrotomaria dixoni sp. nov.

(Pl. 55, figs. 1*a–c*, 2)

1844. ? *Pleurotomaria distincta* Dujard. : Goldfuss, p 75, pl. 187, figs. 1*a–c* (*non* Dujardin).
1850. *Pleurotomaria perspectiva* Mant. : J. de C. Sowerby, *in* Dixon, p. 349, pl. 27, fig. 27 (*non* Mantell sp.).

Material. The holotype (B.M., G.49848) and several paratypes (B.M., S.M.).

Description. Of medium size (maximum diameter *c.* 50 mm.), depressed-turbiniform, with the height about two-thirds of the diameter and the spire angle about 90°. Whorls obtusely angular, with gently sloping outer face and narrower, still more gently sloping ramp. Periphery with a slight, abruptly rounded bulge. Base feebly convex, umbilicus moderately broad. Selenizone, situated at ramp angle rather high on whorl, a relatively wide, convex cord which is smooth except for two or three very faint spiral grooves or threads. Ramp bearing collabral riblets which extend from the suture to more than half-way to ramp angle and are crossed by delicate spiral threads. Whorl outer face and base with numerous fine spiral threads, crossed in places by transverse threads which form a cancellate pattern with, and may produce small granules on, them. At the margin of the umbilicus and on its walls the transverse threads are strengthened and coalesce to form riblets.

Remarks. The relatively wide, strongly convex selenizone, the narrower ramp, and the transverse riblets on it readily distinguish this species from *B. linearis*. The more sharply rounded periphery, which persists in the full-grown shell, distinguishes it from *B. perspectiva*.

Occurrence. Cenomanian, *Holaster subglobosus* Zone of Chalk, Kent, Isle of

Wight, Wiltshire; *Schloenbachia varians* Zone of Chalk, Oxfordshire, Somerset, Dorset; Cenomanian limestone of SE. Devon (type locality, Culverhole).

Bathrotomaria velata (Goldfuss)

(Pl. 54, figs. 3*a–c*, 4)

1844. *Pleurotomaria velata* Goldfuss, p. 76, pl. 187, figs. 2*a–c*.

MATERIAL. Several specimens (B.M., S.M.).

DESCRIPTION. Attaining a fairly large size (diameter of largest specimen *c*. 85 mm.), depressed-turbiniform, with the diameter about twice the height and the spire angle about 120°. Ramp angle obtuse or slightly rounded off, whorl outer face gently sloping, ramp very gently sloping to subhorizontal. Periphery with subangular bulge. Base convex; umbilicus wide. Selenizone a very narrow, convex, transversely ridged cord between two linear grooves at ramp angle; the narrow labral slit to which it corresponds can be seen in some specimens extending back about a third of a whorl from the aperture. Whorl outer face and ramp ornamented with very small granules at the intersections of very narrow, closely arranged spiral cords and collabral threads. Base with numerous narrow spiral cords which are strongly granose near the periphery but only weakly so towards the umbilical opening, where they alternate with narrower threads.

REMARKS. The relatively small specimens from the Cenomanian of Devon, such as the one illustrated in Pl. 54, figs. 3*a–c*, show the undistorted shape of the shell and the delicate sculpture in an uneroded condition. Specimens from the Lower Chalk, such as the one represented in Pl. 54, fig. 4, are larger but distorted; their sculpture agrees well with that of the smaller specimens. These British specimens appear to agree with the description and figure of the species given by Goldfuss, but, if this interpretation of *B. velata* is correct, the species cannot be identical with the higher and more distinctly graduate form, *B. regalis* (Roemer), as suggested by Wollemann (1903 : 83).

OCCURRENCE. Cenomanian, *Holaster subglobosus* Zone, Kent; *Schloenbachia varians* Zone, Sussex; Cenomanian Limestone of SE. Devon.

Bathrotomaria ashburneri sp. nov.

(Pl. 56)

MATERIAL. The holotype (B.M., G.78106, collected by Mr. M. Ashburner) and one paratype (S.M., B.34807).

DESCRIPTION. Moderately large, broadly conical, with the diameter (*c*. 96 mm. in the holotype) exceeding the height and the spire angle slightly less than 90°. Whorls with a very obtuse angulation relatively high on their side, separating a flat or slightly concave outer face from a narrow, rather steeply sloping ramp. Last whorl sharply angular and bulging at periphery. Base flattened-convex, umbilicus broad. Selenizone at ramp angle, moderately wide, concave, bearing very feebly arched, irregularly arranged, thread-like lunulae. Suture bordered on each side by a weak, beaded spiral cord and not readily distinguished. Ornament of remainder of whorl face consisting of numerous fine, closely spaced, unequal spiral threads, crossed by closely spaced collabral threads. Small granules are present at many of the intersections, but there is no regular cancellate pattern. Base ornamented with unequal, weak spiral cords and threads.

REMARKS. The holotype and paratype agree well in the details of the ornament and in the position and characters of the selenizone. The fineness and irregularity of the ornament are very characteristic. In *B. velata* the ornament is more regular, the selenizone narrower, convex, and further from the suture, and the base more strongly convex.

OCCURRENCE. Cenomanian, *Schloenbachia varians* Zone, Lower Chalk, of Chinnor, Buckinghamshire (type locality) and of " Sussex ".

Bathrotomaria perspectiva (Mantell)

(Pl. 58, figs. 1*a–c*, 2, 3*a*, *b* ; Pl. 59, figs. 1*a–c*, 2, 3 ; Pl. 60, fig. 2)

1822. *Cirrus perspectivus* Mantell, p. 194, pl. 18, figs. 12, 21.
1822. *Cirrus depressus* Mantell, p. 195, pl. 18, figs. 18, 22.
1822. *Cirrus granulatus* Mantell, p. 195.
1823. *Cirrus perspectivus* J. de C. Sowerby, p. 35, pl. 428, figs. 1, 2.
1823. *Cirrus depressus* J. de C. Sowerby, p. 35, pl. 428, fig. 3.
1833. *Cirrus perspectivus* Mantell, p. 124, text-figs. *b*, *c*.
1833. *Cirrus depressus* Mantell, p. 124, text-fig. *a*.
1843. *Pleurotomaria perspectiva* Sowerby : d'Orbigny, p. 255, pl. 196.
1844. *Pleurotomaria seriato-granulata* Goldfuss, p. 75, pl. 186, figs. 10*a*, *b*.
1844. *Pleurotomaria granulifera* Münster [MS.] : Goldfuss, p. 76, pl. 187, figs. 3*a*, *b*.
1889. *Pleurotomaria perspectiva* Mant. : Fritsch, p. 74, text-fig. 49.
1896. *Pleurotomaria* (*Leptomaria*) *perspectiva* (Mantell) : Woods, p. 186, pl. 3, figs. 13, 14; pl. 4, fig. 1.
1898. *Pleurotomaria granulifera* Münst. : Müller, p. 86, pl. 11, figs. 10–13.

MATERIAL. Syntype of *Cirrus perspectivus* represented in Mantell's fig. 21, and now designated as lectotype, B.M., G.19057 ; other syntype (Mantell's fig. 12) not traced. Syntype of *Cirrus depressus* represented in Mantell's fig. 18, and now designated as lectotype of that nominal species, B.M., 8622 : other syntype (Mantell's fig. 22) not traced. Holotype of *Cirrus granulatus* (not previously figured), B.M., G.60538. Sowerby's figured specimens of *C. perspectivus*, B.M., G.89524–5, and of *C. depressus*, B.M., 43611. Woods' figured specimens (S.M., B.4273–5). Numerous other specimens.

DESCRIPTION. Of medium size, highly variable in relative height, the most elevated specimens trochiform, with the height about three-quarters of the diameter, the most depressed specimens (Mantell's *Cirrus depressus*) subdiscoidal except for the protruding early whorls. The diameter of the largest shell-bearing specimens referred to the species is 80 mm., but that of a still larger cast retaining the ornament is 104 mm. Earlier whorls obtusely angular, later ones with a strongly convex outline, the evenness of which is modified to a varying extent by the moderately wide, strongly convex, cord-like selenizone, which lies well above mid-whorl and is separated from the suture by a gently inclined, moderately broad ramp, varying from slightly concave to slightly convex. Last whorl usually strongly and evenly convex at periphery in full-grown specimens ; in earlier growth-stages, however, the periphery may be more angular and a peripheral bulge present. Base convex ; umbilicus moderately wide. Selenizone, at least in earlier growth-stages, bearing distinct granules as well as arched, thread-like lunulae. Ramp and whorl outer face ornamented on later whorls (in most specimens) with narrow spiral grooves crossed by collabral grooves, so that the whole surface is cut up into small, lozenge-shaped areas. On the earlier whorls these areas are represented by small granules, the ornament consisting of granose spiral threads, and in occasional specimens the later whorls also have ornament of this type. Base ornamented with concentric cords of unequal strength, most closely spaced near the periphery ; in earlier growth-stages these cords are granose.

REMARKS. The lectotype of *Cirrus perspectivus* is an internal mould, but the strong and even convexity of its last whorl has convinced me of its specific identity with the larger shell-bearing specimens upon which the above description has been based, rather than with any other Chalk species here described. Mantell's holotype of *Cirrus granulatus*, previously unfigured, is illustrated in Pl. 16, fig. 3. In the Sedgwick Museum is a large series of specimens from the Chalk Rock of Cuckhamsley, Berkshire, showing successive stages in growth in which the changes in outline and ornament from shells of the *granulatus* type to those like the one illustrated in Pl. 58, figs. 3*a*, *b* (itself from the Cenomanian) can be followed. The same shells vary greatly in the height of the spire and confirm the conclusion of previous authors that Mantell's *Cirrus depressus* was merely a very depressed individual of the same species as his *C. perspectivus*. The ornament of the later whorls of these depressed shells agrees exactly with that of the corresponding whorls of the most elevated specimens. Their depressed form is not due to deformation in fossilization, as they mostly come from the Chalk Rock, in which the fossils have usually suffered no compression. The nodose selenizone is observable in all the smaller specimens, but the nodes are at the best very obscure in full-grown specimens, possibly owing to erosion. Müller commented on their presence in German specimens referred to *Pleurotomaria granulifera*, the original figure of which much resembles the smaller and similarly ornamented English specimens. Variability in whorl outline among specimens agreeing in the elevation of the spire is shown by shells from the Chalk Rock of Aston Hill, SE. of Aston Rowant, Oxfordshire, and Cuckhamsley, Berkshire. In those from the former locality (Pl. 60, fig. 2) the whorl ramp is distinctly concave, whereas in those from Cuckhamsley (Pl. 58, figs. 3*a*. *b*) it is feebly convex.

Among internal moulds from the Senonian Chalk which most probably belong to *B. perspectiva* are some in which the subangular periphery characteristic of earlier growth stages of Chalk Rock specimens persists in relatively late growth-stages, up to a diameter of 65 mm. in the case of a specimen (B.M., G.79134) from the *Micraster cortestudinarium* Zone of Wiltshire. In the specimen from Bohemia, upon which the species *Pleurotomaria seriatogranulata* Goldfuss was founded, the angular whorl outline and peripheral bulge appear similarly to have persisted to a later growth-stage than in English Turonian specimens, but I consider that this form should be regarded as a synonym of *B. perspectiva.*

The angularity of the whorl outline, although usually confined to the earlier whorls, justifies the inclusion of this species in *Bathrotomaria* rather than in *Leptomaria.* It differs from *B. dixoni* in its broader sutural ramp and in the absence of transverse riblets on the ramp.

Occurrence. Upper Albian (top of Upper Greensand), Weymouth (doubtful specimen). Cenomanian Limestone, Seaton, Devon. Cenomanian (Lower Chalk) of Lewes, Sussex (type locality of *Cirrus granulatus*) and Bridport, Dorset. Turonian (especially Chalk Rock or equivalent horizon) of Kent, Sussex, Berkshire, Wiltshire, Hertfordshire, Oxfordshire, and Bedfordshire. Lower Senonian (*Micraster cortestudinarium* and *M. coranguinum* Zones) of Kent, Sussex, Wiltshire, and Yorkshire (mainly internal moulds).

Bathrotomaria regalis (Roemer)

(Pl. 57, figs. 1*a–c*, 3)

1841. *Trochus regalis* Roemer, p. 81, pl. 12, fig. 7.
1889. *Pleurotomaria regalis* (Roemer) : Griepenkerl, p. 71.
1898. *Pleurotomaria regalis* (Roem.) : Müller, p. 85, pl. 11, figs. 7, 8.
1903. *Pleurotomaria regalis* (Roemer) : Wollemann, p. 83, pl. 3, fig. 8.
1921. *Pleurotomaria regalis* (Roem.) : Ravn, p. 30, fig. 5.

Material. Several specimens (B.M., S.M., G.S.M.).

Description. Moderately large, gradate-conical, diameter of largest specimen (*c.* 80 mm.) approximately equal to its original height, although some specimens are more depressed. Whorls with vertical or almost vertical, flat to slightly concave outer face separated by a well-marked angulation from a wide, gently sloping ramp. Last whorl subangular at periphery. Base moderately convex, umbilicus narrow. Selenizone at ramp angle, convex, relatively narrow. Ornament consisting of numerous spiral threads and cords which, on the best preserved specimen, can be seen to be crossed by fine, close-set collabral grooves, producing small granulations on the cords.

Remarks. Griepenkerl and Müller have included *Pleurotomaria velata* Goldfuss in the synonymy of this species, but the form here identified as *Bathrotomaria velata* is much more depressed and broadly umbilicate, with a gently inclined whorl outer face, while the spiral element of its ornament is not predominant, as in the present specimens.

Occurrence. Lower Cenomanian, *Schloenbachia varians* Zone, of St. Lawrence, Isle of Wight. Upper Cenomanian, *Holaster subglobosus* Zone, of Folkestone and Dover (Grey Chalk) and of Wendover Canal, near Little Tring, Hertfordshire. Upper Senonian, *Belemnitella mucronata* Zone, Norwich. Roemer stated that the type specimen of *Trochus regalis* came from the " untere Kreide ". Müller, however, recorded the species from the Lower Senonian, and Griepenkerl, Wollemann and Ravn from the Upper Senonian.

Genus ***CONOTOMARIA*** Cox, 1959

TYPE SPECIES. *Pleurotomaria mailleana* d'Orbigny, 1843.

GENERIC CHARACTERS. Conical, anomphalous to broadly phaneromphalous; whorls flat or slightly sigmoidal in outline, last whorl with sharply angular, often bulging periphery; selenizone at or above mid-whorl, quite close to suture in some species, not coinciding with an angulation; predominant ornament spiral cords.

Conotomaria gigantea (J. de C. Sowerby)

1836. *Pleurotomaria striata* Fitton, p. 153; also explan. of pl. 14, fig. 16.
1836. *Pleurotomaria gigantea* J. de C. Sowerby, p. 339, pl. 14, fig. 16.
1850. *Pleurotomaria fittoni* d'Orbigny, p. 70 (new name for *P. striata* Fitton, considered a secondary homonym of *Helix striata* J. Sowerby (*non* Roemer)).
1858. *Pleurotomaria gigantea* Sow.: Pictet & Renevier, p. 38, pl. 4, fig. 5.
1900. *Pleurotomaria gigantea* Sow.: Wollemann, p. 148.

MATERIAL. Numerous specimens. The holotype has not been traced.

DESCRIPTION. Large (diameter up to about 165 mm.), conical; mostly with diameter slightly less than height and spire angle about 70°; some specimens, however, are more depressed, possibly owing to deformation in fossilization. Whorls flat or almost so, the last with sharply angular, scarcely bulging periphery and flattened or concave base; no umbilicus. Selenizone relatively narrow, slightly above mid-whorl, its detailed structure unknown. Whorl face and base ornamented with numerous unequal spiral bands and depressed cords; there may be as many as twenty on the whorl face below the selenizone, the number above the latter being smaller. Collabral ornament apparently confined to growth-rugae, although no specimens have been seen with the finer ornamental details preserved.

REMARKS. There appears to have been some indecision regarding the name under which this species was to be described. Of the two specific names originally published, *gigantea* is the one that has been generally adopted.

OCCURRENCE. Aptian, Hythe Beds, of Kent. Lower Aptian, Ferruginous Sands, *Tropaeum bowerbanki* Zone, of Isle of Wight. Records of the species from Switzerland and Germany seem reliable.

Conotomaria seendensis sp. nov.

(Pl. 47, figs. 2*a*–*d*)

MATERIAL. The holotype (G.S.M., 44656); also two specimens (G.S.M., 44657–8) too imperfect to rank as paratypes.

DESCRIPTION. Small, regularly conical, diameter (*c.* 18·5 mm. in holotype) only slightly exceeding height, spire angle rather less than 90°. Whorls flat, the last abruptly rounded at periphery, which has a slight bulge. Base flattened, not well exposed; umbilicus probably absent. Selenizone at mid-whorl, flush, of moderate width, its detailed structure not preserved. Ornament of spiral cords, about eight on whorl face below selenizone and six above it, overridden by weaker, evenly and closely spaced collabral threads.

Occurrence. Upper Aptian, *Parahoplites nutfieldensis* Zone, Seend, Wiltshire.

Conotomaria lamplughi sp. nov.

(Pl. 48, figs. 5*a–c*)

Material. The holotype (S.M., B.24567) and one paratype (B.M., G.89503, C. W. Wright Coll.).

Description. Small, regularly conical, diameter (*c.* 24 mm. in paratype, the larger specimen) almost equal to height, spire angle about 70°. Whorls flat, the last abruptly rounded at periphery, which has a pronounced bulge not overlapped on the penultimate whorl. Base flattened ; no umbilicus. Selenizone at mid-whorl, of moderate width, flush, with a median and bordering threads, but without pronounced lunulae. Whorl face ornamented with spiral threads (four of primary strength above selenizone and about ten below it, with weaker intercalaries on last whorl), crossed by rather unevenly spaced collabral threads, which produce a fine cancellate pattern and small nodes on the spirals, particularly above selenizone. Base with similar cancellate ornament.

Remarks. This species much resembles *C. seendensis*, but has a more acute apex, a less pronounced peripheral bulge and (apparently) a somewhat more coarsely cancellate ornament.

Occurrence. Lower Albian, Shenley Limestone, Shenley Hill, Bedfordshire.

Conotomaria folkestonensis sp. nov.

(Pl. 49, figs. 4*a*, *b*)

Material. The holotype only (B.M., G.89482).

Description. Of small-medium size, conical, with the diameter (*c.* 30 mm.) probably exceeding the height (the lower part of the shell is obscured by matrix) and the spire angle slightly more than 90°. Whorls with a flat outer face inclined in conformity with the general slope of the spire and a very narrow, subhorizontal or gently inclined sutural ledge or ramp. Selenizone at ramp angle, very high on whorl side, convex, with weak tubercles. Whorl outer face bearing numerous fine spiral threads ; sutural ledge with about six rather coarser threads. Collabral ornament, of delicate threads, is confined to the sutural ramp and to the lower part of the outer face.

Remarks. The presence of a distinct ramp angle is unusual in *Conotomaria*, but the conical form of the shell and the high position of the selenizone suggest that it is with this genus that the species has closest affinity.

Occurrence. Albian, Gault Clay (bed uncertain) of Folkestone, Kent.

Conotomaria chardstockensis sp. nov.

(Pl. 50, figs. 11, 12*a–c*)

MATERIAL. The holotype (B.M., G.3422), a specimen lacking the apical whorls but retaining the original shell on most of the last whorl, and several internal moulds assumed to belong to the same species.

DESCRIPTION. Of small-medium size, high-conical, the height (*c.* 33 mm. in the largest specimen) considerably exceeding the diameter and the spire angle about 50°. Whorls almost flat, the last sharply rounded at periphery, with flattened base ; no umbilicus. Selenizone narrow, impressed, almost at mid-whorl. Whorl face with about seven flattened spiral cords below selenizone, but smooth above it except for a low, broad swelling adjoining the suture. Base with numerous spiral cords.

REMARKS. The internal mould of *Pleurotomaria thurmanni* Pictet & Roux (1849 : 230, pl. 22, fig. 1), Albian of Switzerland, is rather similar in shape, but the shell is very differently ornamented. *P. fleuriausa* d'Orbigny (1843 : 265, pl. 201, figs. 5, 6), Cenomanian of France, has whorls which are sigmoidal in outline and bear spiral cords above as well as below the selenizone.

OCCURRENCE. Cenomanian of Chardstock, Dorset (type-locality), and of Warminster, Maiden Bradley, and Devizes, Wiltshire.

Conotomaria percevali sp. nov.

(Pl. 57, figs. 2*a*, *b*)

MATERIAL. The holotype (B.M., G.23029, presented by S. G. Perceval, Esq.) and one paratype (B.M., G.89504, C. W. Wright Coll.). Also two internal moulds, possibly referable to the species.

DESCRIPTION. Moderately large, conical, with the height (originally *c.* 80 mm. in the largest specimen, the paratype) almost equal to the diameter and the spire angle slightly exceeding 60°. Whorls quite flat except in the paratype, in which the last whorl tends to develop an ill-defined shoulder near the aperture. Last whorl subangular at periphery. Base very feebly convex ; umbilicus narrow. Selenizone high on whorl side, one-fifth to one-quarter of breadth of whorl from upper suture, narrow, flush, between spiral threads, and separated from suture by a smooth band. Whorl face below selenizone bearing four broad, flat spiral bands with narrower intervals each occupied by a spiral thread. Base ornamented with only slightly unequal spiral bands with narrow, relatively deep intervals.

REMARKS. *Pleurotomaria marrotiana* d'Orbigny (1843 : 267, pl. 202, figs. 5, 6) was based on an internal mould of a *Conotomaria* much resembling the present species in shape and size, but as its selenizone and surface ornament have not been described it is uncertain if it is a closely related form. The high position of the selenizone is very characteristic of the present species.

OCCURRENCE. Cenomanian Limestone " near Axmouth, Devon " (type-locality) and Whitlands, Devon (probably the same bed, queried by C. W. Wright as " top of Bed A " [of Jukes-Browne], and possibly almost the same locality). Internal moulds, possibly of this species, from the Cenomanian of Sidmouth, Devon and of Warminster, Wiltshire.

Conotomaria mailleana (d'Orbigny)

(Pl. 52, figs. 1*a–c*, 2)

1843. *Pleurotomaria mailleana* d'Orbigny, p. 253, pl. 195.
1867. *Pleurotomaria mailleana* d'Orb. : Guéranger, p. 10, pl. 12, unnumbered fig.; pl. 13, fig. 1.

MATERIAL. Five specimens (B.M.), two fairly complete.

DESCRIPTION. Of medium size, depressed-conical, diameter (80 mm. in largest specimen) slightly less than twice the height, spire angle *c.* 110°. Whorl outline sigmoidal, convex above, concave below ; periphery angular, bulging to a moderate extent. Base moderately to strongly convex ; umbilicus broad. Selenizone rather high on whorl face, where whorl outline changes from convex to concave, its detailed structure not preserved in the specimens now recorded. Whorl face ornamented with fine spiral grooves (clearly preserved in present material only on a small part of surface of one specimen) ; base with concentric cords and threads which mostly alternate in strength.

REMARKS. The specimens agree well with the figures of French Cenomanian specimens cited above. This species bears a slight resemblance to *Bathrotomaria linearis* (Mantell), the most obvious differences lying in the position of its selenizone, which is at mid-whorl in that species, and in its more angular and bulging periphery. *Pleurotomaria supercretacea* Favre (1869 : 51, pl. 8, figs 17*a–c*) from Galicia seems a closely related species.

OCCURRENCE. Cenomanian Limestone, Seaton, Devon. Cenomanian basement bed, Snowdon Hill, Chard, Somerset. The species is also recorded from Warminster and the Isle of Wight by the Geological Survey (Jukes-Browne & Hill, 1900 : 463 ; 1904 : 473), but I have seen no specimens from these localities.

Conotomaria laticarinata sp. nov.

(Pl. 53, figs. 1*a–c*)

MATERIAL. The holotype only (B.M., G.89505, C. W. Wright Coll.).

DESCRIPTION. Rather large, the diameter (originally *c.* 110 mm. in the holotype) much exceeding the height, and the spire broadly conical, with an angle of about 110°. Whorls sigmoidal in outline, with the greater part of their face rather strongly concave, the convex part narrow, forming a sutural ledge. Periphery with a very broad, attenuated keel. Base strongly convex, umbilicus wide. Selenizone at edge of sutural ledge, very close to suture, and consisting of a moderately convex median cord separated by grooves from narrow lateral cords. Outer face of whorls ornamented with numerous fine grooves, separating spiral threads which are crossed by very weak, opisthocline collabral threads. Base ornamented with shallow spiral grooves which are closely arranged near the periphery and more distant near the umbilical opening; weak spiral cords are present on the umbilical walls.

Remarks. This species seems related to *Conotomaria mailleana* (d'Orbigny), described above, and to *C. formosa* (Leymerie) (d'Orbigny, 1843: 259, pl. 199, figs. 1, 2), differing from both in the close proximity of its selenizone to the suture, its broader peripheral keel, and its more strongly convex base.

Occurrence. Cenomanian Limestone (probably top of Bed A of Jukes-Browne), Whitlands, near Seaton, Devon.

Genus ***PLEUROTOMARIA*** Defrance, 1826 (*sensu lato*)

The following species of Pleurotomariidae do not agree with any of the genera (*Pleurotomaria*, *Leptomaria*, *Bathrotomaria*, *Conotomaria*) to which the species described above belong, but it has not been thought desirable to found further genera for their reception. They are, therefore, referred to *Pleurotomaria, sensu lato.*

Pleurotomaria spilsbyensis sp. nov.

(Pl. 44; Pl. 45, fig. 1)

Material. The holotype (B.M., G.4351) and one paratype (S.M., B.11696).

Description. Large (diameter of holotype 117 mm.), depressed-turbiniform, with low, obtuse spire. Last whorl with a steep, flattened-convex outer face not sharply separated from a broad, gently sloping, convex upper face. Periphery broadly rounded; base strongly convex; umbilicus broad, open, bordered by an obtuse angulation. Selenizone high on outer face of whorls, very wide, strongly concave, with deep, parabolic lunulae. Adjoining the slightly channelled suture, and bordered on its outer side by a shallow groove, is a broad, ill-defined spiral swelling crossed by short, obscure collabral ribs. No other spiral ornament is visible except an ill-defined cord which is just exposed above the suture near the aperture and forms the margin of the base. Collabral rugae conspicuous and irregular; they form the only ornament on the base.

Occurrence. Neocomian, Berriasian, Spilsby Sandstone, Lincolnshire. The locality of the holotype, collected by J. E. Lee, is not recorded, but its matrix is identical with that of the paratype, which comes from Donnington.

Pleurotomaria anstedi Forbes

(Pl. 47, figs. 1*a*–*d*)

1845. *Pleurotomaria anstedi* Forbes, p. 349, pl. 5, fig. 1.

Material. The holotype (G.S.M., 2235) and a few other specimens.

Description. Moderately large (diameter up to 80 mm.), depressed-turbiniform, with a low, dome-like spire in which the early whorls have an almost discoidal coiling ; height of shell slightly less than two-thirds of diameter. Face of whorls evenly and strongly convex ; periphery with a not very prominent, cord-like bulge, which remains exposed on the later spire whorls. Base moderately convex ; umbilicus broad, bordered by an ill-defined, obtuse ridge. Selenizone wide, strongly convex, situated well above mid-whorl, and bearing irregular, well-arched lunulae. Ornament consisting of numerous irregular spiral threads and cords which may undulate unevenly and are absent from the base. No collabral ornament except irregular rugae.

Remarks. This appears to be a species of very local distribution, and records from other countries seem to be based on misidentifications. Thus a specimen from the Lower Cretaceous of the Swiss Jura figured as *P. anstedi* by Pictet & Campiche (1863, pl. 80, fig. 3) is wrongly named, as is also, most probably, an internal mould from the Neocomian of Germany figured by Weerth (1884, pl. 7, fig. 12).

Occurrence. Upper Aptian, Sandgate Beds, *Parahoplites nutfieldensis* Zone, Fuller's Earth, of Nutfield, Surrey (type locality) and of Redhill, Surrey. Dr. R. Casey tells me that the species occurs also in the Hythe Beds, although there are no specimens from this formation in the collections examined.

Pleurotomaria allobrogensis Pictet & Roux

(Pl. 50, figs. 1*a*, *b*)

1849. *Pleurotomaria allobrogensis* Pictet & Roux, p. 240, pl. 23, fig. 3.

Material. Several specimens (B.M., S.M.).

Description. Obtusely conical internal moulds of medium size (diameter *c*. 45 mm.) in which the feebly convex whorls are encircled by three strong, rounded spiral cords, the last corresponding to the peripheral bulge of the last whorl. The selenizone appears to have been located on the middle one of these cords. In the specimens now recorded the uppermost cord fades away on the last whorl and does not reach the aperture.

Remarks. This species was founded on internal moulds from the Albian Greensand of the Geneva district. Although the ornament of the actual shell is still undescribed, the species (unlike most) can be readily recognized from its internal mould, and I refer the specimens now recorded to it without hesitation. It has already been cited in Cambridge Greensand species lists.

Occurrence. Uppermost Albian, Cambridge Greensand, of the Cambridge district. Upper Cenomanian, Grey Chalk, Dover (B.M.).

Pleurotomaria glyndensis sp. nov.

(Pl. 53, figs. 2*a*–*c*)

Material. The holotype only (B.M., 88804).

Description. Of small-medium size (diameter of holotype 30 mm., but part of last whorl is broken away), sublenticular, with low, obtuse spire. Whorls with flattened outer face, a rounded shoulder, and a very narrow, subhorizontal sutural ramp. Periphery rounded, base moderately convex; umbilicus rather narrow. Selenizone at mid-whorl, well below shoulder, narrow, almost flush, slightly nodose, distinguishable only with difficulty between the tuberculate spiral cords (three above it, four on whorl face below it) that constitute the ornament. Base with a relatively small number of tuberculate spiral cords which, except near the periphery, are regularly spaced and separated by intervals of greater width; a weak spiral cord occupies the middle of some of the intervals.

REMARKS. This shell is more coarsely granose than specimens of *Bathrotomaria perspectiva* of comparable size, and differs in the position of its selenizone, well below the ramp angle. Compared with *P. galliennei* d'Orbigny (1843 : 256, pl. 197), from the French Cenomanian, it differs in that its granules are smaller and not transversely aligned, and in the ornament of its base.

OCCURRENCE. Cenomanian, *Schloenbachia varians* Zone, Lower Chalk, of Glynde, near Lewes, Sussex.

Species Represented Only by Internal Moulds to which Specific Names are Not Assigned

Pleurotomaria A

(Pl. 52, fig. 3)

MATERIAL. Several specimens (B.M.).

DESCRIPTION. Broadly conical moulds of medium size (maximum diameter 45 mm.) in which the diameter much exceeds the height and the whorls and periphery are of very strong and even convexity.

REMARKS. These specimens agree well with *P. laharpi* Pictet & Campiche (1863 : 437, pl. 80, fig. 5), founded on similar internal moulds from the Upper Gault of Switzerland.

OCCURRENCE. Cenomanian, Upper Greensand, Warminster, Wiltshire.

Pleurotomaria B

(Pl. 50, fig. 3)

MATERIAL. Several specimens (B.M., S.M.).

DESCRIPTION. Coeloconoid moulds of medium size (maximum diameter 41 mm.), in which the diameter only slightly exceeds the height, the convexity of the whorls is very slight, and the periphery is angular. A sutural ledge appears on the last whorl.

REMARKS. These specimens were the basis of Jukes-Browne's (1875 : 308) record of *P. laharpi* from the Cambridge Greensand, but they differ from that species in their coeloconoid spire, flatter whorls and angular periphery. They are more like *P. vectensis*, sp. nov., but in that species the spire is lower and not coeloconoid.

OCCURRENCE. Upper Albian, Cambridge Greensand.

Pleurotomaria C

(Pl. 50, fig. 4)

MATERIAL. Several specimens (S.M., B.M.).

DESCRIPTION. Broadly conical, trochiform moulds of large-medium size in which the diameter (60 mm. in the largest specimens) well exceeds the height and the whorls have a steeply sloping outer face, a rounded shoulder, and a narrow sutural ledge. The periphery is subangular.

REMARKS. Seeley (1861 : 294) listed specimens of this species as *P. neocomiensis* d'Orbigny, and Jukes-Browne (1875 : 293, 308) as *P. vraconensis* Pictet & Campiche (1863 : 443, pl. 81, fig. 3). Specimens listed by Jukes-Browne (1875 : 308) as *P. jukesii* Seeley (see p. 419) do not appear to be separable from them. In the true *P. vraconensis*, from the Upper Gault of Switzerland, the outer face of the whorls is steeper, the sutural shelf wider and the periphery less angular. The present specimens seem closer to *P. plicata* (J. Sowerby) (see p. 394) but are larger and rather more depressed than that species.

OCCURRENCE. Upper Albian, Cambridge Greensand.

Pleurotomaria D

(Pl. 50, fig. 2)

MATERIAL. Several specimens (B.M., S.M.).

DESCRIPTION. Sublenticular, depressed moulds of medium size (maximum diameter 40 mm.), in which the whorls have a flattened-convex outer face inclined at an angle of about 60° with the horizontal, a narrow sutural ledge, and subangular periphery.

REMARKS. Specimens of this species in the Sedgwick Museum were recorded by Jukes-Browne (1875 : 294, 308) under the name *P. rouxi* d'Orbigny (1850 : 132). D'Orbigny erected the species in question for the unfigured form misidentified by Pictet & Roux (1849 : 244) as *P. fittoni* Roemer (1841 : 82, pl. 12, fig. 10). As the only published figures of *P. rouxi*, those of Renevier (1868, pl. 6, figs. 10, 11), are of imperfect specimens and are of little help in the identification of the species, it is not obvious how Jukes-Browne identified English specimens with it. The internal moulds now described closely resemble the one figured by Pictet & Campiche (1863 : 440, pl. 81, figs. 2*a*–*c*) under the name *P. moreausiana* d'Orbigny, although this seems to have been quite distinct from d'Orbigny's species.

OCCURRENCE. Upper Albian, Cambridge Greensand.

Pleurotomaria E

(Pl. 50, fig. 6)

MATERIAL. Several specimens (B.M., S.M.).

DESCRIPTION. Depressed-turbiniform moulds of small-medium size (maximum diameter 32 mm.) in which the diameter is about twice the height and the sloping whorl face is strongly convex, with a narrow sutural ledge. The periphery is rather abruptly rounded.

REMARKS. This form was listed by Jukes-Browne (1875 : 294, 308) as *P. rhodani* (Brongniart). The figures of that species published by Brongniart (1822 : 96, pl. 9, fig. 8) and by Pictet & Roux (1849, pl. 24, fig. 1) are of a *Leptomaria* with strongly and evenly convex whorls, from the Albian of the Perte du Rhône, near Bellegarde. D'Orbigny (1843, pl. 192, figs. 7, 8) figured under the same name an internal mould with more numerous whorls than Brongniart's species. The present internal moulds could conceivably belong to the true *P. rhodani*, but their identity cannot be established definitely.

OCCURRENCE. Upper Albian, Cambridge Greensand.

Pleurotomaria F

(Pl. 50, fig. 5)

MATERIAL. Several specimens (B.M., S.M.).

DESCRIPTION. Depressed-cyrtoconoid, almost lenticular moulds of large-medium size (maximum diameter 62 mm.), with the face of the whorls feebly convex and inclined to the horizontal at an angle of about 50°. Periphery angular.

REMARKS. This form was listed by Seeley (1861 : 294) as *P. brongniartiana* ? d'Orbigny and by Jukes-Browne (1875 : 308) as *P. lima* d'Orbigny (1843 : 248, pl. 192, figs. 1–3). The outline of the internal mould is rather like d'Orbigny's fig. 3 (except that the peripheral bulge is less distinct), but the largest of d'Orbigny's specimens is only 33 mm. in diameter. It is most probable, therefore, that the present species is distinct from *P. lima*. There is also a rather close resemblance to the internal mould upon which d'Orbigny (1843 : 271, pl. 205, figs. 1, 2) founded the species *P. espaillaciana*, but the periphery of the present form is not quite so sharp as in that specimen.

OCCURRENCE. Upper Albian, Cambridge Greensand.

Pleurotomaria G

(Pl. 50, fig. 7)

MATERIAL. Four specimens (B.M.).

DESCRIPTION. Trochiform moulds of medium size (maximum diameter 41 mm.) in which the diameter is somewhat in excess of the height and the whorls have a steeply sloping, only slightly convex face on which two spiral swellings, one quite close to the suture, are visible. The periphery is subangular.

REMARKS. These moulds differ from those recorded above as "*Pleurotomaria* C" in the narrowness of their sutural ledge (which was probably absent on the original shell), in their slightly greater height, and in the presence of the two spiral swellings. They are more elevated than in *P. allobrogensis*, in which two comparable swellings are present.

OCCURRENCE. Upper Albian, Cambridge Greensand.

Pleurotomaria [*Conotomaria*?] H

(Pl. 60, fig. 3)

MATERIAL. One specimen (B.M., G.16517).

DESCRIPTION. A large, conical internal mould lacking the apical whorls. Its original height (*c.* 140 mm.) was well in excess of the diameter (*c.* 110 mm.) and its spire angle is about 45°. The whorls are almost flat-sided and are subangular at the periphery, the later ones imbricating slightly. There are obscure indications of a selenizone situated at mid-whorl.

REMARKS. This specimen is probably a *Conotomaria*, but the position of the selenizone shows that it does not belong to *C. percevali*. It could belong to *C. marrotiana* (d'Orbigny) (1843 : 267, pl. 202, figs. 5, 6), which was, however, founded on a much smaller internal mould without imbricating whorls. The position of the selenizone in *C. marrotiana* is, moreover, uncertain, and the type-specimen of the species seems to have come from beds of Senonian age.

OCCURRENCE. Cenomanian, Newington, near Folkestone, Kent.

Pleurotomaria [*Conotomaria* ?] I

(Pl. 60, figs. 1*a*, *b*)

MATERIAL. Three specimens (B.M.).

DESCRIPTION. Trochiform internal moulds, the largest about 105 mm. in diameter, in which the diameter somewhat exceeds the height, the outer face of the whorls is flat or slightly concave and very steep, and there is a narrow, almost horizontal sutural ledge. The periphery is subangular.

Preserved with the internal mould here figured is an oyster valve found associated with it by A. W. Rowe, its collector. Although the exact position which it occupied cannot be ascertained, this valve evidently grew attached to the last whorl of the gastropod by almost its entire surface and, while the gastropod shell has now disappeared by solution in the course of fossilization, the attachment area of the oyster reproduces its ornament in negative very clearly (Pl. 60, fig. 1*b*). The selenizone, with the growth-lines sweeping back to it, is seen to have been high on the feebly convex, unangulated whorl side, and to have been bordered above and below by almost smooth bands. The lower half of the whorl side is occupied by closely spaced spiral cords separated by intervals of about their own width, while four spiral ridges near the upper edge of the oyster (which presumably coincided with the position of the suture) represent grooves on the original shell.

REMARKS. The more elevated of the internal moulds now recorded are very similar to the much smaller specimen figured by Müller (1898, pl. 11, fig. 9) as *Pleurotomaria subgigantea* d'Orbigny. The figure of Goldfuss (1844, pl. 187, figs. 6*a–c*) upon which d'Orbigny's species was founded represents a *Conotomaria* in which the selenizone is lower on the whorl side than in the form now described (according to the evidence of the oyster valve) and the spiral cords are weaker. The form now described was almost certainly also a *Conotomaria*, the sutural shelf present on the internal mould resulting, presumably, from a relatively thick shell, as the oyster valve gives no indication of its presence on the exterior of the actual shell.

OCCURRENCE. Senonian, *Micraster cortestudinarium* Zone, of Kent. Upper Senonian of Norwich, Norfolk.

SPECIES NOT ACCEPTED, OR TRANSFERRED TO OTHER FAMILIES

Trochus bicarinatus J. Sowerby

1818. *Trochus bicarinatus* J. Sowerby, p. 39, pl. 221, fig. 2.
1840. *Pleurotomaria bicarinata* J. de C. Sowerby, Index, p. 10.

Sowerby stated that the holotype (B.M., 43638) came from Marcham Field, Oxfordshire, a well-known locality for Corallian fossils. It appears to be wrongly localized, as its matrix contains grains of glauconite and is probably Upper Greensand. The species, referred to *Pleurotomaria*, is recorded with a query from the " Chloritic Marl " of Maiden Bradley in the catalogue of the Geological Survey Collection (E. T. Newton, 1878 : 74). There is no trace of a selenizone on the small amount of shell retained by the holotype, and I think that the species belongs to the group of Cretaceous forms which Cossmann (1916 : 140) includes in the genus *Nummocalcar*.

Pleurotomaria jukesii Seeley

1864. *Pleurotomaria jukesii* Seeley, p. 92, pl. 8, figs. 10, 11.

This species was founded on a specimen in the Brighton Museum from the Chalk of an unrecorded locality. Its description was illustrated by two crude line drawings, and it was said to be distinguishable from *P. perspectiva* (Mantell) by its few whorls. The holotype, evidently a *Bathrotomaria*, cannot now be traced in the collection of the Brighton Museum, and the identity of the species, if distinct from *P. perspectiva*, is not obvious. The species must, therefore, of necessity be ignored. Internal moulds from the Cambridge Greensand which Jukes-Browne (1875 : 308) identified as *P. jukesii* are here (p. 416) recorded as " *Pleurotomaria* C ".

Trochus laevis Pulteney

1813. *Trochus laevis* Pulteney, p. 108, fig. 11 of pl.
1940. *Pleurotomaria laevis* (Pulteney) : Cox, p. 126, pl. 7, fig. 11.

This species was founded on an internal mould from the Upper Greensand of Melbury, near Shaftesbury, Dorset. The type specimen cannot now be traced, but clearly closely resembled internal moulds of *Bathrotomaria perspectiva*, the earliest occurrence of which here recorded (with some doubt) is in the Upper Greensand of Weymouth. Pulteney's name *laevis* remains available should future collecting show that the Upper Greensand form is distinct from *B. perspectiva*. It would, however, be undesirable for it to replace the name *perspectiva* if they prove to be identical.

Pleurotomaria semiconcava Seeley

1861. *Pleurotomaria semiconcava* Seeley, p. 291, pl. 11, fig. 17.

This species (holotype, S.M., B.38726) was founded on a small internal mould from the Cambridge Greensand. I can observe no trace of a selenizone, although Seeley's description mentions a " keel of the sinus ". The specimen most probably belongs to the genus *Semisolarium*.

Pleurotomaria thomsoni Tate

1843. *Turbo? bicarinatus* Sowerby MS. : Portlock, p. 421 (four prior homonyms already existed).
1865. *Pleurotomaria thomsoni* Tate, p. 37.

The holotype (G.S.M., 52447) is a littoriniform internal mould retaining small portions of the inner layers of the shell. There is no trace of a selenizone and the shape of the specimen is unlike that of any pleurotomariid. Woods (1896 : 89) records having examined it and come to the conclusion that it is the internal mould of a shell related to his species *Turbo geinitzi*. I fully agree with his remarks. The specimen came from the Upper Chalk of Co. Derry, Northern Ireland.

UNCONFIRMED OR REJECTED RECORDS

(Queried or qualified identifications have been omitted, and only the most important published lists of species have been examined.)

brongniartiana d'Orbigny. Record : Chloritic Marl of North Wiltshire (Jukes-Browne & Hill, 1903 : 163 ; also 1904 : 473, queried from several areas). The Wiltshire record may refer to *Leptomaria hindei* sp. nov. (p. 400).

cassisiana d'Orbigny. Records : Cenomanian of Dorset, Somerset and Devon (Jukes-Browne & Hill, 1903 : 113, Eggardon Hill ; Jukes-Browne & Hill, 1904 : 473). Cenomanian of Reigate (Davis, 1923 : 132). These records probably refer to *Bathrotomaria dixoni* sp. nov. (p. 404).

greppini Pictet & Campiche. Record : Albian (" Gaize ") of Devizes, Wiltshire (E. T. Newton, 1878 : 61 ; Jukes-Browne & Hill, 1900 : 256, 463). The species was founded on the internal mould of a *Conotomaria* from the Middle Neocomian. The record from Devizes probably refers to a form known only as an internal mould and not described in the present paper.

guerangeri d'Orbigny. Record : Cenomanian of Lewes, Sussex (Jukes-Browne & Hill, 1904 : 473). This record may refer to *Bathrotomaria linearis* (Mantell).

laharpi Pictet & Campiche. Record : Cambridge Greensand (Jukes-Browne, 1875 : 308, and subsequent works). See " *Pleurotomaria* B " of the present paper (p. 415).

lima d'Orbigny. Record: Cambridge Greensand (Jukes-Browne, 1875 : 308). See "*Pleurotomaria* F" of the present paper (p. 417).

matheroniana d'Orbigny. Record: Cenomanian (Chloritic Marl) of Devizes and Maiden Bradley, Wiltshire (Jukes-Browne & Hill, 1904 : 473). The record probably refers to *Conotomaria chardstockensis* sp. nov. (p. 411).

moreausiana d'Orbigny. Records: Cenomanian (Chloritic Marl) of Isle of Wight (Bristow, 1889 : 278; Jukes-Browne & Hill, 1904 : 473). The records probably refer to *Pleurotomaria rockenensis* sp. nov. (p. 395).

neocomiensis d'Orbigny. Records: Cambridge Greensand (Seeley, 1861 : 294); see "*Pleurotomaria* C" of the present paper (p. 416). Atherfield Clay of Pease Marsh and Shalford, near Guildford (Topley, 1875 : 421); no specimens of Pleurotomariidae from this formation have been seen by the present writer.

regina Pictet & Roux. Record: Cambridge Greensand (Jukes-Browne, 1877 : 499, and subsequent works). Specimens in the Sedgwick Museum said to be the basis of this record belong to *P. allobrogensis* Pictet & Roux. The original figures of *P. regina* published by Pictet & Roux (1849, pl. 24, figs. *2a–g*) seem to represent two different species. Figs. *2a–d* represent a specimen which retains its shell and is quite unlike any form found in the Cambridge Greensand.

rhodani (Brongniart). Records: Upper Greensand of Eastbourne, Sussex, and Petersfield and Alton, Hampshire (Topley, 1875 : 430). Upper Greensand, Devizes (Newton, 1878 : 61). Warminster Greensand (Jukes-Browne & Hill, 1900 : 463). Chloritic Marl, Isle of Wight (Bristow, 1889 : 278). Cambridge Greensand (Jukes-Browne, 1875 : 294, 308, and later works). For the Cambridge Greensand form, see "*Pleurotomaria* E" (p. 416). No suggestion can be made as to the species to which the other records refer.

rouxi d'Orbigny. Records: Cambridge Greensand (Jukes-Browne, 1875 : 294, 308, and later works). Chloritic Marl, Devizes, Wiltshire (Newton, 1878 : 75). For the Cambridge Greensand form, see "*Pleurotomaria* D" (p. 416). I cannot suggest to what species the other record refers.

vraconnensis Pictet & Campiche. Record: Cambridge Greensand (Jukes-Browne, 1875 : 293, 308, and later works). See "*Pleurotomaria* C" of the present paper (p. 416).

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PLATE 44

Pleurotomaria spilsbyensis sp. nov.

Holotype (B.M., G.4531). Neocomian, Berriasian, Spilsby Sandstone; Lincolnshire. Apertural and apical views (× 1). Page 413.

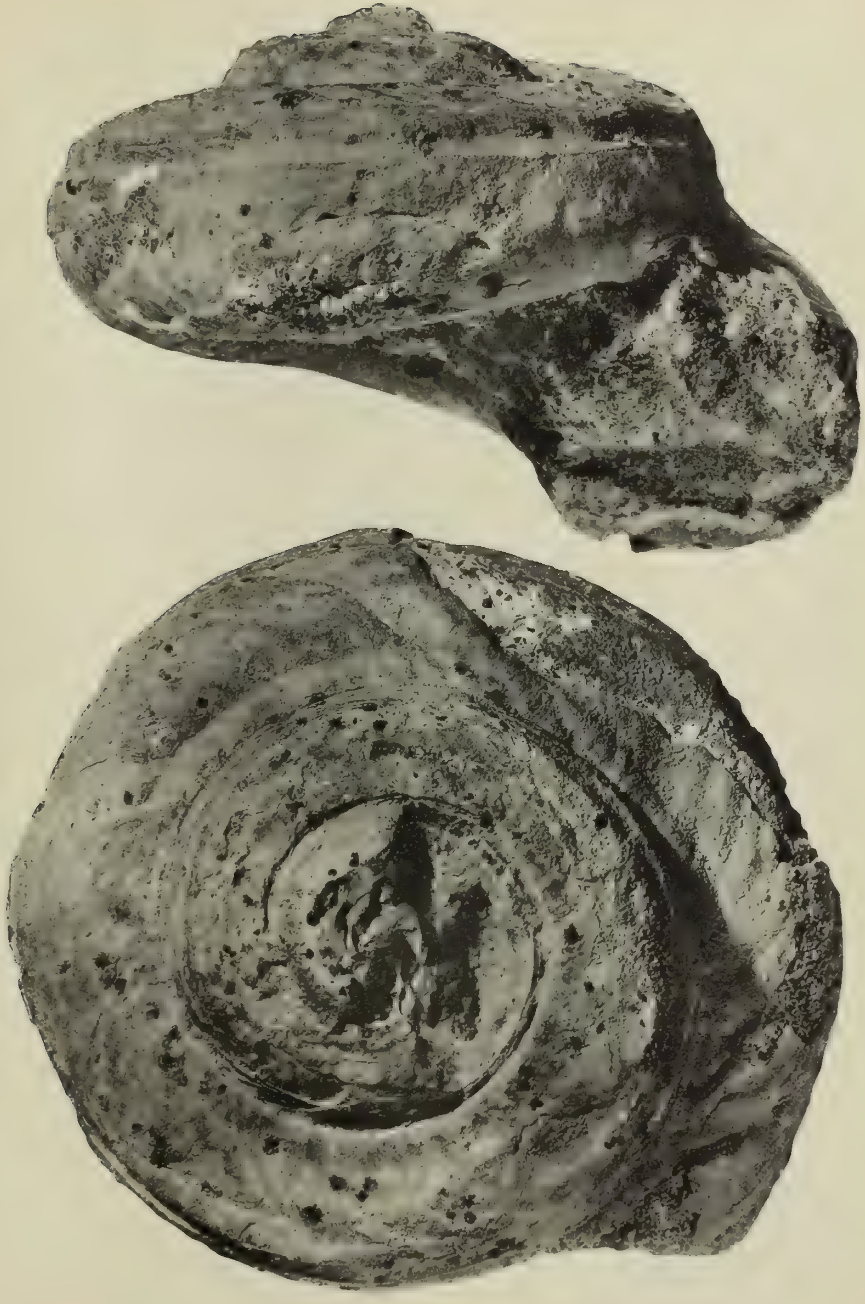


PLATE 45

Pleurotomaria spilsbyensis sp. nov.

FIG. 1. Paratype (S.M., B.11696). Neocomian, Berriasian, Spilsby Sandstone; Donnington, Lincolnshire. Base (× 1). Page 413.

Bathrotomaria swinnertoni sp. nov.

FIGS. 2*a*, *b*. Holotype (B.M., G89485). Neocomian, Hauterivian, Claxby Ironstone; Nettleton Top Mine, Lincolnshire. (*a*) Apertural view (× 1); (*b*) abapertural view (× 2·7). Page 401.

Bathrotomaria swinnertoni sp. nov.

FIG. 3. Paratype (B.M., G.89486). Neocomian, Hauterivian, Claxby Ironstone; Nettleton Top Mine, Lincolnshire. Part of last whorl, viewed in direction normal to slope of side of shell (× 4).

Bathrotomaria wrighti sp. nov.

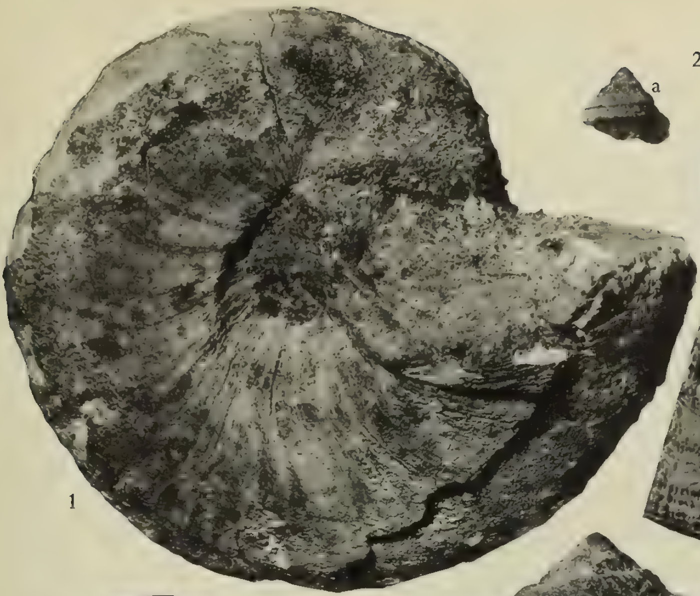
FIGS. 4*a–d*. Holotype (B.M., G.89484). Neocomian, Hauterivian, Claxby Ironstone; Nettleton Top Mine, Lincolnshire. (*a*, *b*, *c*) Apertural, basal and apical views (× 1); (*d*) part of last whorl, viewed in direction normal to slope of side of shell (× 2). Page 400.

Bathrotomaria speetonensis sp. nov.

FIG. 5. Holotype (B.M., G55232). Neocomian, Hauterivian, Bed C4 of Speeton Clay; Speeton, Yorkshire. Apertural view (× 1); the specimen lacks most of the spire. Page 402.

Bathrotomaria speetonensis sp. nov.

FIGS. 6*a*, *b*. Paratype (G.S.M., 96773). Neocomian, Speeton Clay; Speeton, Yorkshire. Side and upper surface of last whorl (× 1·5); the rest of the specimen is missing.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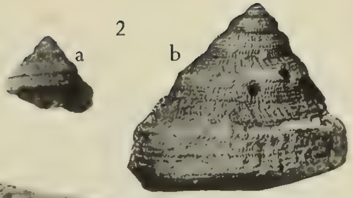
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a
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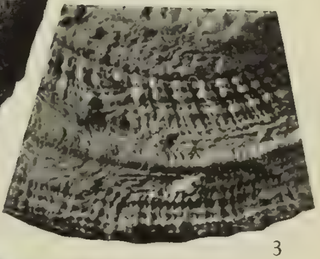
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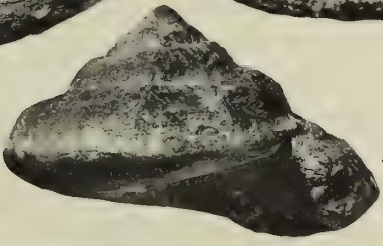
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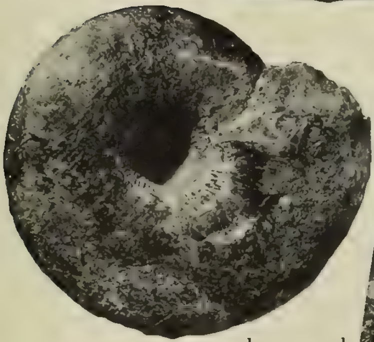
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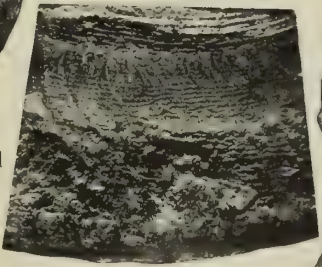
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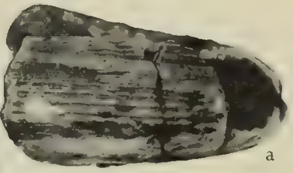
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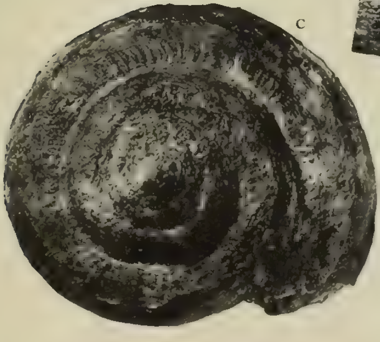
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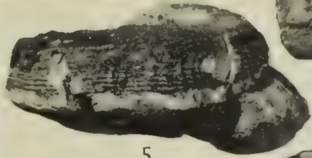
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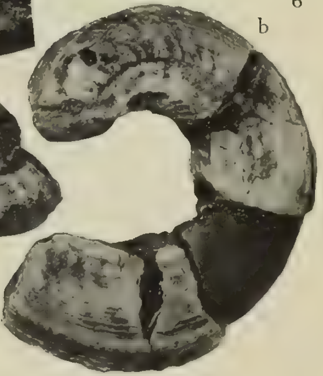
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PLATE 46

Bathrotomaria nettletonensis sp. nov.

FIGS. 1*a–c*. Holotype (B.M., G.89487). Neocomian, Hauterivian, Lower Tealby Clay; Nettleton Top Mine, Lincolnshire. (*a*, *b*) Apertural and abapertural views (× 1); (*c*) part of last whorl, viewed in direction normal to slope of side of shell (× 2). Page 401.

Bathrotomaria atherfieldensis sp. nov.

FIGS. 2*a*, *b*. Holotype (B.M., G.432). Lower Aptian, top of Atherfield Clay, Lower Lobster Bed; Atherfield, Isle of Wight. (*a*) Abapertural view (× 1); (*b*) part of last whorl, viewed in direction normal to slope of side of shell (× 2·6). Page 402.

Leptomaria donningtonensis sp. nov.

FIG. 3. Holotype (S.M., B.11676). Neocomian, Hauterivian, Tealby Limestone; Donnington, Lincolnshire. Abapertural view (× 1). Page 396.

Leptomaria donningtonensis sp. nov.

FIG. 4. Paratype (S.M., B.11677). Neocomian, Hauterivian, Tealby Limestone; North Willingham, Lincolnshire. Side of shell, viewed in direction normal to its slope (× 3); the specimen is partly crushed.

Pleurotomaria toulmini sp. nov.

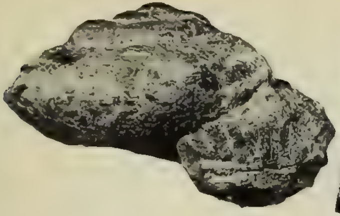
FIG. 5. Squeeze made from holotype (B.M., G.89481), a natural mould of the exterior of the shell. Aptian, Hythe Beds; probably Kent (× 1). Page 392.

Bathrotomaria ferruginea (Keeping)

FIG. 6. Topotype (B.M., 66365). Lower Aptian; Potton, Bedfordshire (× 1). Page 402.

Leptomaria willinghamensis sp. nov.

FIGS. 7*a*, *b*. Holotype (S.M., B.11675). Neocomian, Hauterivian, Tealby Limestone; North Willingham, Lincolnshire. (*a*) Apertural view (× 1); an oyster adheres to side of shell; (*b*) side of shell, viewed in direction normal to its slope (× 2). Page 396.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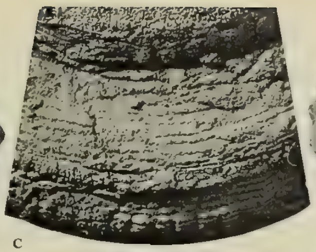
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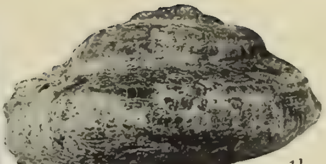
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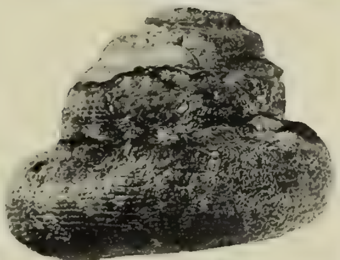
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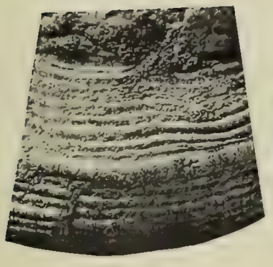
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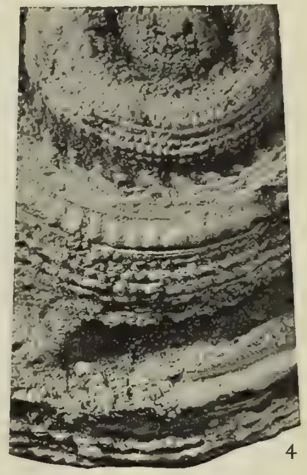
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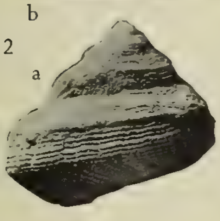
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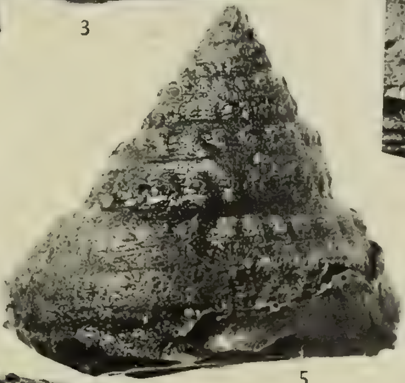
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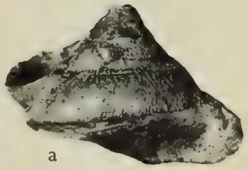
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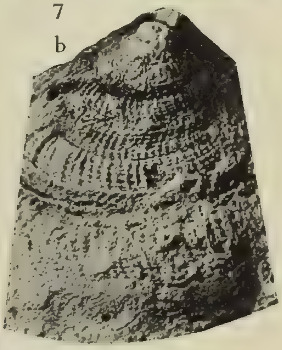
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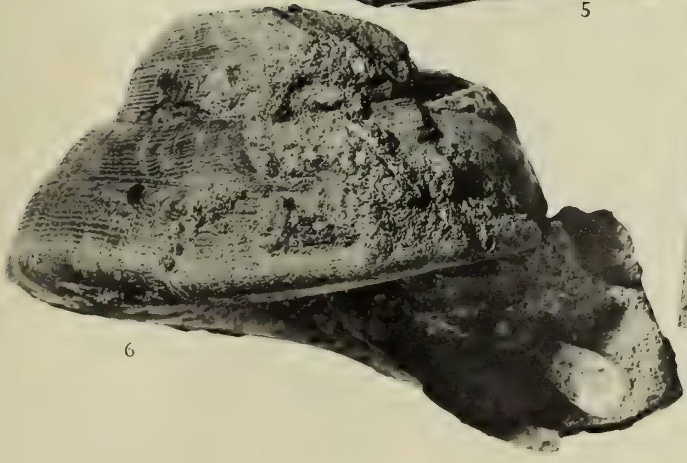
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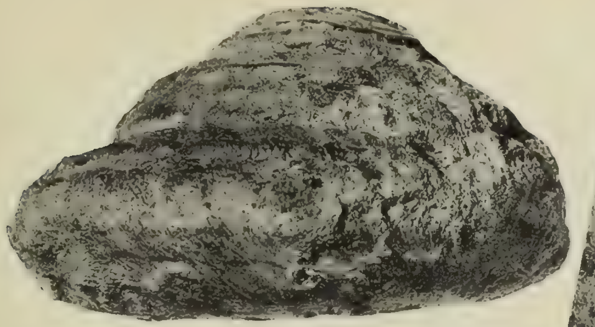
PLATE 47

Pleurotomaria anstedi Forbes

FIGS. 1*a–d*. (B.M., G.72334.) Aptian, Sandgate Beds, *Parahoplites nutfieldensis* Zone; Park Pit, north of Nutfield Priory, Surrey. (*a*, *b*, *c*) Abapertural, apertural and basal views (× 1); (*d*) part of side of shell, viewed in direction normal to its slope (× 1·4). Page 413.

Conotomaria seendensis sp. nov.

FIGS. 2*a–d*. Holotype (G.S.M., 44656). Upper Aptian, *Parahoplites nutfieldensis* Zone; Seend, Wiltshire. (*a*) Apertural view (× 1); (*b*, *c*) abapertural and basal views (× 1·5); (*d*) part of penultimate and last whorls, viewed in direction normal to slope of side of shell (× 4); the penultimate whorl retains traces of ornament on its lower half and of the selenizone at mid-height. Page 409.



a

1

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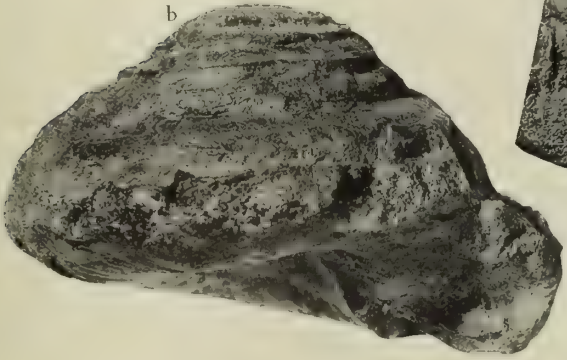

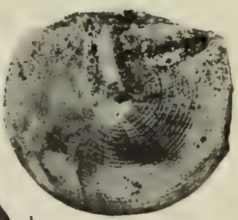

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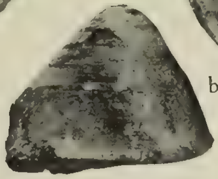

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2

a

1c

2d

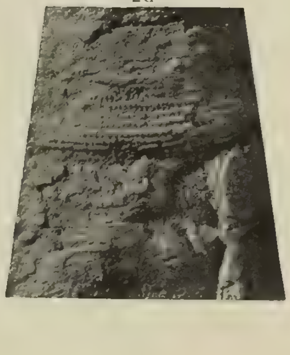


PLATE 48

Pleurotomaria campichei Keeping

FIGS. 1*a–c*. Holotype (S.M., B.19297). Aptian; Upware, near Cambridge. (*a*) Apertural view (× 1); (*b*, *c*) basal and abapertural views (× 1·5). Page 393.

Pleurotomaria campichei Keeping

FIG. 2. Topotype (G.S.M., 96771). Aptian; Upware, near Cambridge. Side of shell, viewed in a direction normal to its slope (× 2·7).

Bathrotomaria leightonensis sp. nov.

FIGS. 3*a*, *b*. Paratype (B.M., G.89489). Lower Albian, *Leymeriella subregularis* Subzone; Arnold's Pit, Billington Crossing, near Leighton Buzzard, Bedfordshire. (*a*) Squeeze from natural mould, abapertural view (× 1); (b) another squeeze from same natural mould, part of side of shell, viewed in a direction normal to its slope (× 3·2). Page 403.

Bathrotomaria leightonensis sp. nov.

FIG. 4. Holotype (B.M., G.89488). Same occurrence as preceding specimen. Abapertural view (× 1).

Conotomaria lamplughi sp. nov.

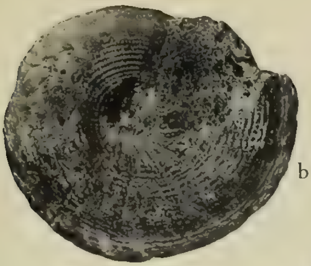
FIGS. 5*a–c*. Holotype (S.M., B.24567). Lower Albian, Shenley Limestone; Shenley Hill, Bedfordshire. (*a*) Apertural view (× 1); (*b*) abapertural view (× 1·5); (*c*) part of side of shell, viewed in a direction normal to its slope (× 4·5). Page 410.

Pleurotomaria shenleyensis sp. nov.

FIGS. 6*a–d*. Holotype (S.M., B.24566). Lower Albian, Shenley Limestone; Shenley Hill, Bedfordshire. (*a*) Apertural view (× 1); (*b*, *c*) abapertural and basal views (× 1·5); (*d*) side of shell, viewed in a direction normal to its slope (× 3). Page 393.

Leptomaria billingtonensis sp. nov.

FIGS. 7*a–d*. Holotype (B.M., G.65274). Lower Albian, *Leymeriella subregularis* Subzone; Arnold's Pit, Billington Crossing, near Leighton Buzzard, Bedfordshire. (*a*, *b*, *c*) Abapertural, apertural and basal views (× 1); (*d*) part of side of last whorl, viewed in a direction normal to its slope (× 3·5). Page 397.



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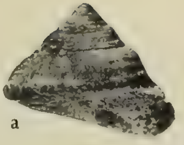

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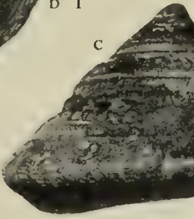

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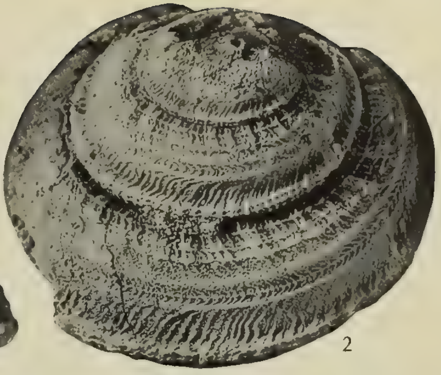

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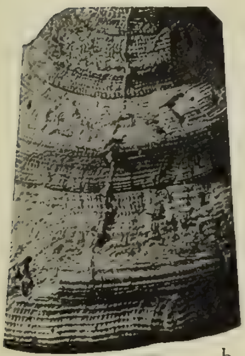

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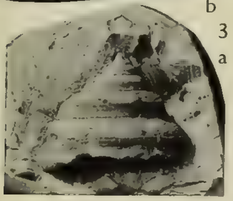

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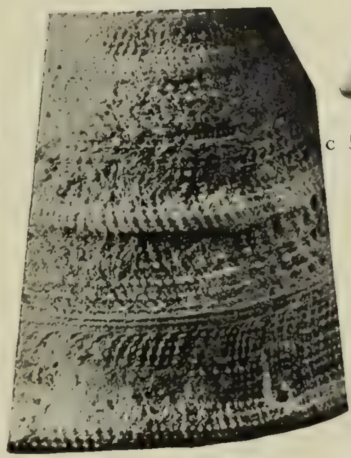

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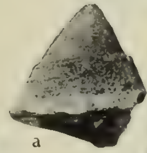

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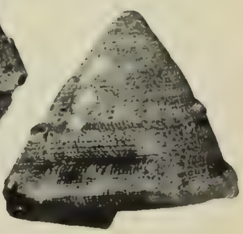

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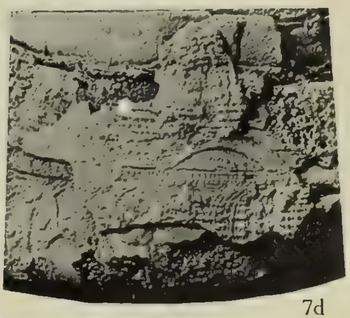

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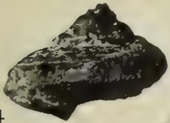

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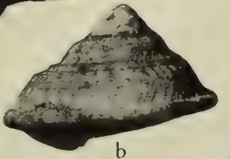

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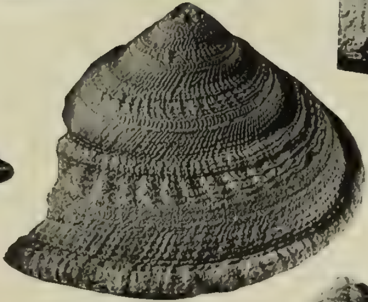

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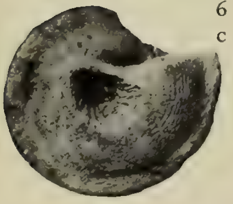

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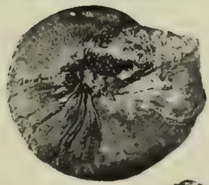

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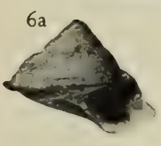

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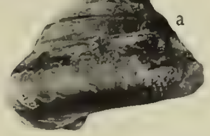

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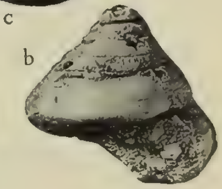


b

PLATE 49

Leptomaria gibsi (J. Sowerby)

FIG. 1. (B.M., G.55140.) Lower Middle Albian, *Douvilleiceras mammillatum* Zone; Gatehouse Pit, Grovebury, Leighton Buzzard, Bedfordshire. Squeeze from natural mould of exterior of shell (× 2·5). Page 397.

Leptomaria gibsi (J. Sowerby)

FIGS. 2*a*, *b*. Holotype (B.M., 43630), a specimen lacking the outer shell-layer. Lower Middle Albian, *Douvilleiceras mammillatum* Zone, Lower Gault; Folkestone, Kent. (*a*) Apertural view (× 1); (*b*) abapertural view (× 1·5).

Leptomaria gibsi (J. Sowerby)

FIG. 3. Topotype (G.S.M., 98564). Same occurrence as the preceding specimen. Small portion of surface of shell, on which original ornament is preserved (× 5); the suture crosses the middle of the figure.

Conotomaria folkestonensis sp. nov.

FIGS. 4*a*, *b*. Holotype (B.M., G.89482). Albian, Gault; Folkestone, Kent. (*a*) Apertural view (× 1); (*b*) part of surface of two whorls, viewed in a direction normal to slope of side of shell (× 2·5); the sutural ramp forms a light band near the top and, again, at the middle of the figure. Page 410.

Pleurotomaria plicata (J. Sowerby)

FIG. 5. Holotype (B.M., 43631). Albian, Gault; Folkestone, Kent. Internal mould, apertural view (× 1). Page 394.

Pleurotomaria plicata (J. Sowerby)

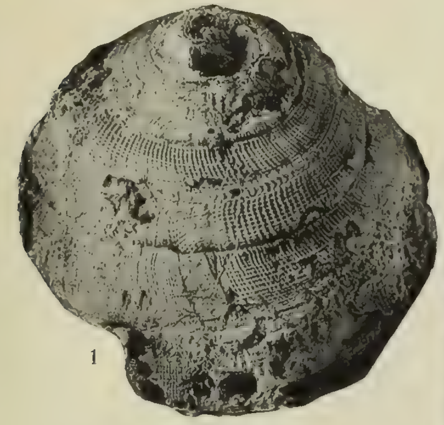
FIGS. 6*a*, *b*. Topotype (B.M., G.4883). Upper Middle Albian, *Dipoloceras cristatum* Subzone, Gault; Folkestone, Kent. (*a*) Apical view (× 1); (*b*) part of surface of two whorls, viewed in a direction normal to slope of side of shell (× 2·8).

Pleurotomaria plicata (J. Sowerby)

FIGS. 7*a–c*. Topotype (B.M., G.89483). Same occurrence as preceding specimen. Apertural, basal and abapertural views (× 1).

Leptomaria pricei sp. nov.

FIGS. 8*a–c*. Holotype (S.M., B.31837). Albian, Gault; Folkestone, Kent. (*a*, *b*) Apertural and abapertural views (× 1); (c) part of side of shell, viewed in a direction normal to its slope (× 2·9). Page 398.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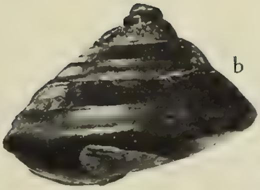
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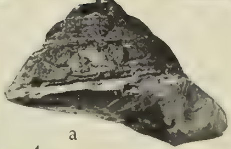
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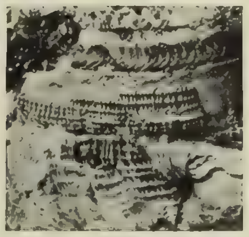
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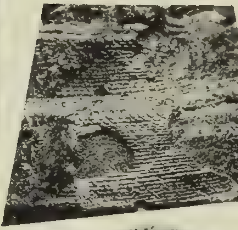
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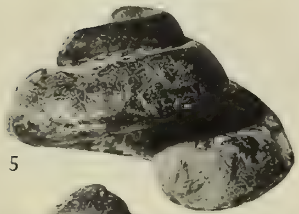
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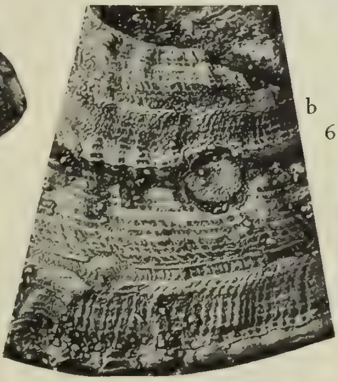
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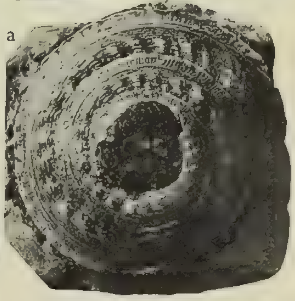
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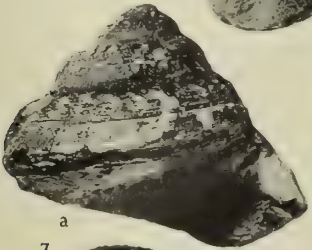
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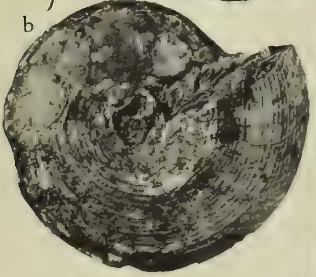
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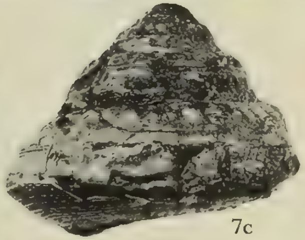
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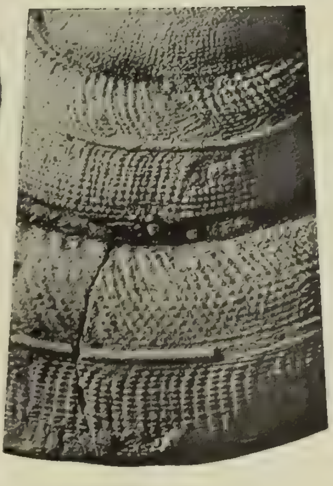
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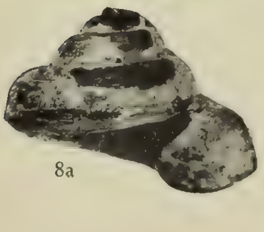
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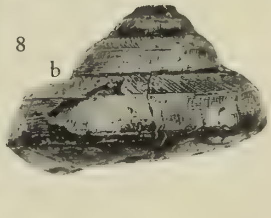
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PLATE 50

Pleurotomaria allobrogensis Pictet & Roux

FIGS. 1*a*, *b*. (S.M., B.38734.) Upper Albian, Cambridge Greensand; Cambridge district. Internal mould, apertural and apical views (× 1). Page 414.

Pleurotomaria D

FIG. 2. (B.M., G.8767.) Upper Albian, Cambridge Greensand; Cambridge district. Internal mould, abapertural view (× 1). Page 416.

Pleurotomaria B

FIG. 3. (S.M., B.38881.) Upper Albian, Cambridge Greensand; Cambridge district. Internal mould, apertural view (× 1). Page 415.

Pleurotomaria C

FIG. 4. (S.M., B.38745.) Upper Albian, Cambridge Greensand; Cambridge district. Internal mould, abapertural view (× 1). Page 416.

Pleurotomaria F

FIG. 5. (B.M., G.82334.) Upper Albian, Cambridge Greensand; Cambridge district. Internal mould, apertural view (× 1). Page 417.

Pleurotomaria E

FIG. 6. (S.M., B.38769.) Upper Albian, Cambridge Greensand; Cambridge district. Internal mould, abapertural view (× 1). Page 416.

Pleurotomaria G

FIG. 7. (B.M., G.3419.) Upper Albian, Cambridge Greensand; Cambridge district. Internal mould, abapertural view (× 1). Page 417.

Pleurotomaria vectensis sp. nov.

FIG. 8. (B.M., G.90870.) Lower Cenomanian, *Schloenbachia varians* Zone, Glauconitic Marl; St. Lawrence, Isle of Wight. Internal mould, apertural view (× 1). Page 394.

Pleurotomaria vectensis sp. nov.

FIG. 9. (B.M., 88896.) Lower Cenomanian; Warminster, Wiltshire. Internal mould, apertural view (× 1).

Pleurotomaria vectensis sp. nov.

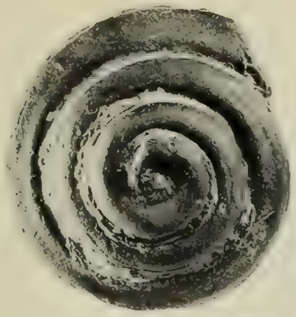
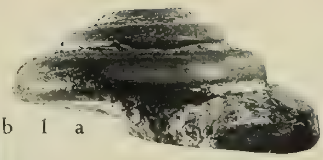
FIGS. 10*a–c*. Holotype (B.M., G.3421). Lower Cenomanian, *Schloenbachia varians* Zone, Glauconitic Marl; Sand Rock Spring, near Chale, Isle of Wight. (*a*) Apertural view (× 1); (*b*) base (× 1·5); (*c*) two whorls, viewed in a direction normal to slope of side of shell (× 2·6).

Conotomaria chardstockensis sp. nov.

FIG. 11. (B.M., 88898.) Cenomanian; Devizes, Wiltshire. Internal mould, apertural view (× 1). Page 411.

Conotomaria chardstockensis sp. nov.

FIGS. 12*a–c*. Holotype (B.M., G.3422). Cenomanian; Chardstock, Dorset. (*a*) Abapertural view (× 1); (*b*) base (× 1·3); (*c*) part of last two whorls, viewed in a direction normal to slope of side of shell (× 3); the suture is in the middle of the figure.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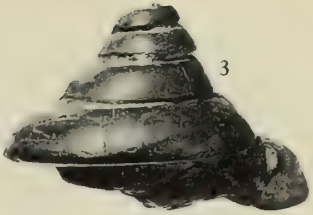
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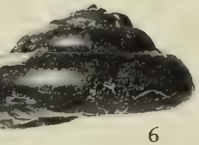
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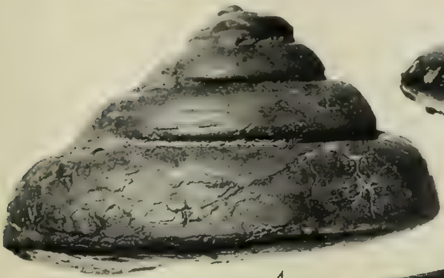
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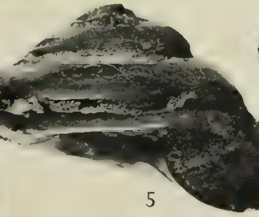
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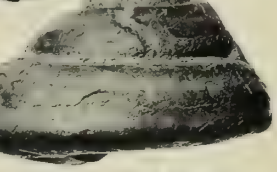
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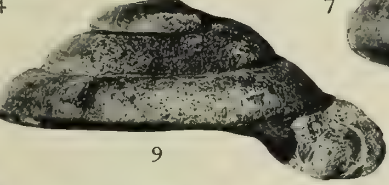
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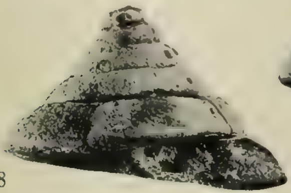
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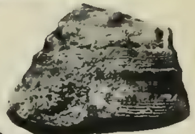
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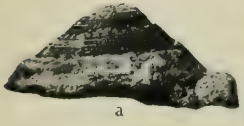
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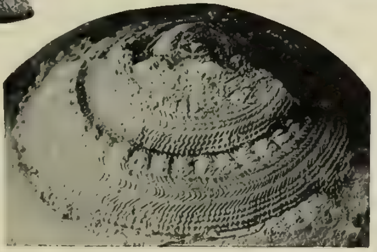
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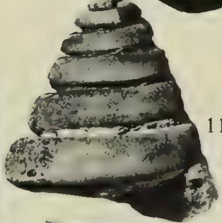
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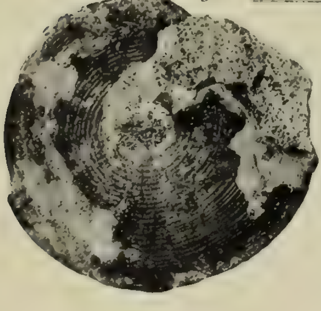
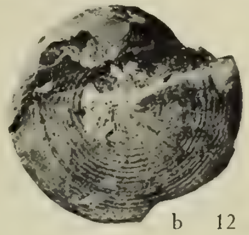
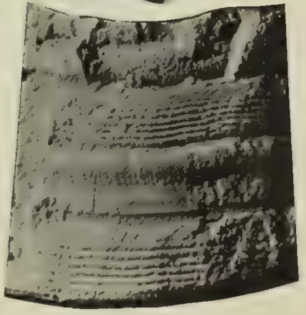



b 12 c

PLATE 51

Leptomaria hindei sp. nov.

FIGS. 1*a–c*. Holotype (B.M., G.27577). Cenomanian Limestone ; probably of South Devon. (*a*, *b*) Abapertural and basal views (× 1) ; (*c*) part of last whorl, viewed in a direction normal to slope of side of shell (× 1·7). Page 400.

Pleurotomaria rockenensis sp. nov.

FIGS. 2*a–c*. Holotype (B.M., G.89490). Lower Cenomanian, *Schloenbachia varians* Zone. Glauconitic Marl ; Rocken End, Isle of Wight. (*a*) Apertural view (× 1) ; (*b*) base (× 1·4) ; (*c*) part of last whorl, viewed in a direction normal to slope of side of shell (× 3). (Page 395).

Pleurotomaria rockenensis sp. nov.

FIG. 3. Paratype (S.M., B.62656). Lower Cenomanian, *Schloenbachia varians* Zone, Glauconitic Marl ; Ventnor, Isle of Wight. Apertural view (× 1).

Pleurotomaria rockenensis sp. nov.

FIGS. 4*a*, *b*. Paratype (B.M., G.429). Lower Cenomanian, *Schloenbachia varians* Zone, Glauconitic Marl ; Isle of Wight. Internal mould, apertural and apical views (× 1).

Leptomaria wilmingtonensis sp. nov.

FIG. 5. Paratype (B.M., G.89494). Cenomanian Limestone ; Wilmington, near Honiton, Devon. Side of shell, viewed in a direction almost normal to its slope (× 2). Page 399.

Leptomaria wilmingtonensis sp. nov.

FIGS. 6*a*, *b*. Holotype (B.M., G.89495). Same occurrence as preceding specimen. Abapertural and basal views (× 1).

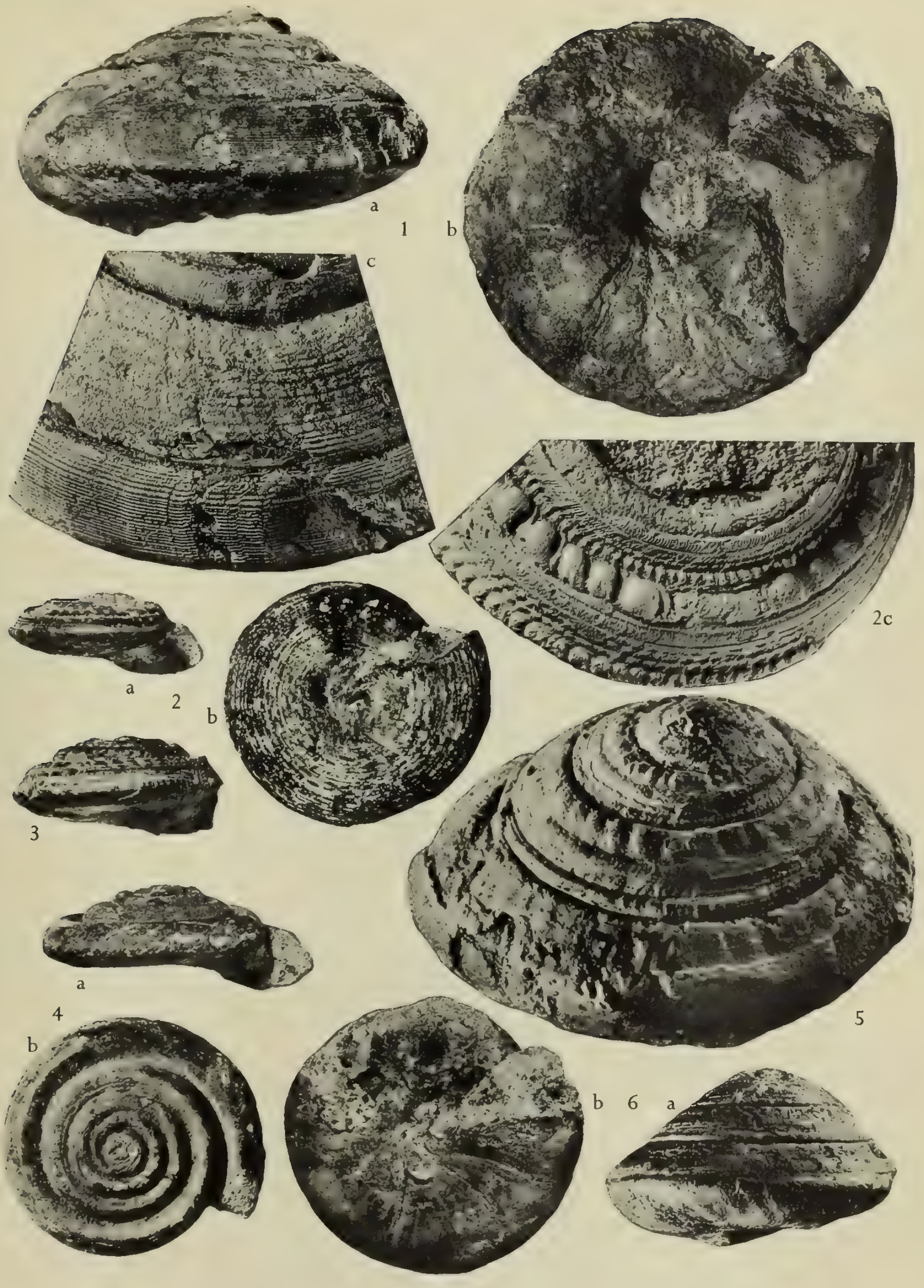

a
1
b
c
2c
a
2
b
3
a
4
b
5
b
6
a

PLATE 52

Conotomaria mailleana (d'Orbigny)

FIGS. 1*a–c*. (B.M., G.49915.) Cenomanian Limestone; 2 miles east of Seaton, Devon. (*a*, *b*) Apertural and basal views (× 1); (*c*) part of side of shell, viewed in a direction normal to its slope (× 2); the suture, which is rather obscure, is seen towards the top and, again, at the middle of the figure; the selenizone, which is more conspicuous, is seen at about one-third of the whorl-width below it. Page 412.

Conotomaria mailleana (d'Orbigny)

FIG. 2. (B.M., G.89506.) Cenomanian Basement Bed; Snowdon Hill, Chard, Somerset. Apertural view (× 1); the specimen is almost an internal mould.

Pleurotomaria A

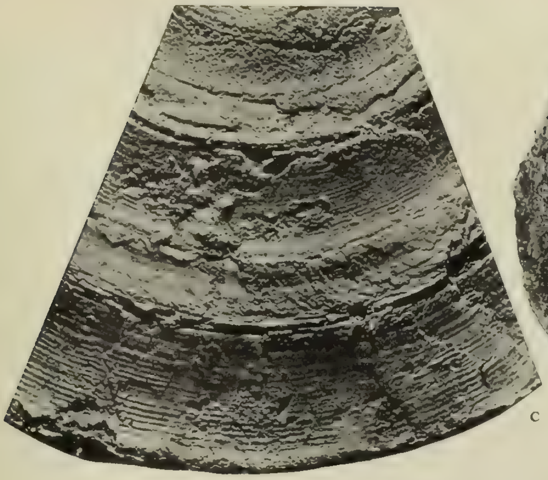
FIG. 3. (B.M., 32617.) Cenomanian; Warminster, Wiltshire. Internal mould, abapertural view (× 1). Page 415.

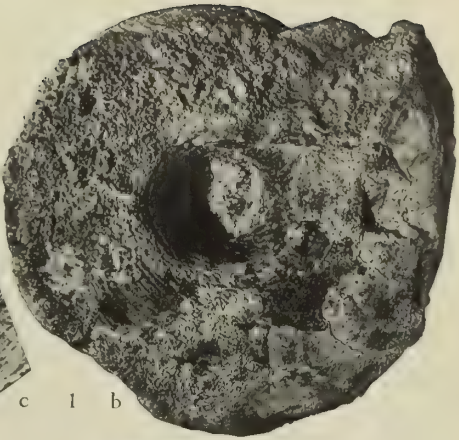
Leptomaria axmouthensis sp. nov.

FIGS. 4*a*, *b*. Paratype (S.M., B.34826). Cenomanian Limestone; Axmouth, near Seaton, Devon. Apertural and basal views (× 1). Page 399.

Leptomaria axmouthensis sp. nov.

FIGS. 5*a*, *b*. Holotype (S.M., B.34824). Same occurrence as preceding specimen. (*a*) Abapertural view (× 1); (*b*) part of side of shell, viewed in a direction normal to its slope (× 3); rather more than three whorls are seen.





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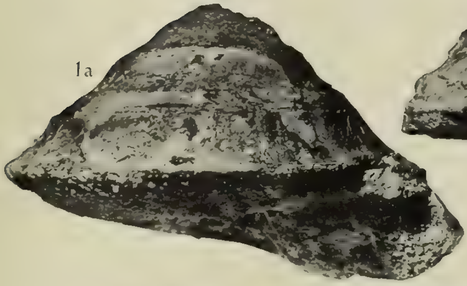

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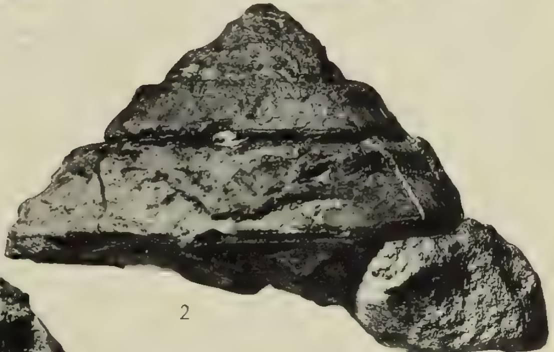

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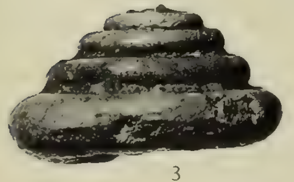

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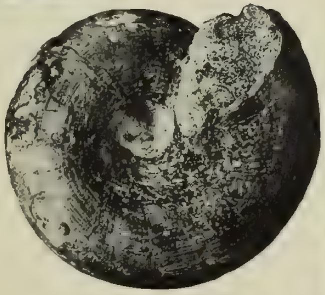
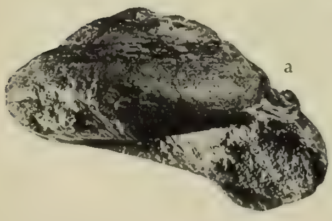
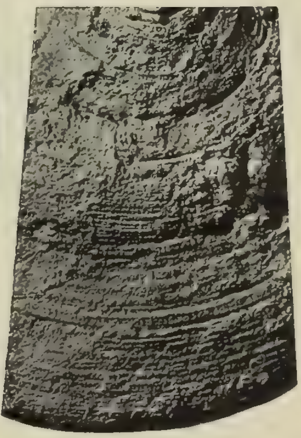
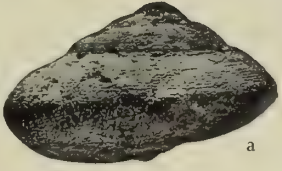




a 4 b





a 5 b

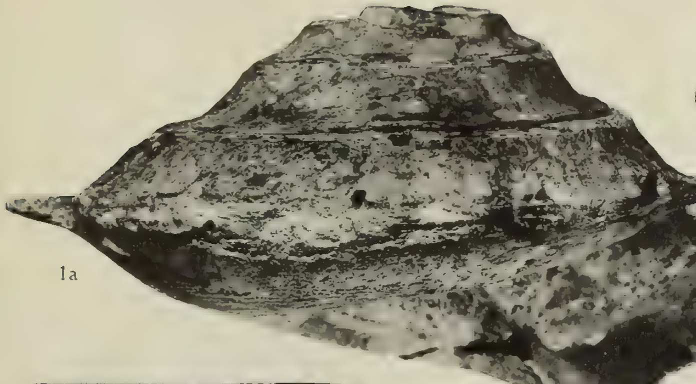
PLATE 53

Conotomaria laticarinata sp. nov.

FIGS. 1*a–c*. Holotype (B.M., G.89505). Cenomanian Limestone ; Whitlands, near Seaton, Devon. (*a*, *b*) Apertural and basal views (× 1) ; (*c*) part of penultimate whorl, viewed in a direction normal to slope of side of shell (× 2) ; the adapical suture is the narrow groove seen near the top of the figure, and the selenizone lies between the two conspicuous grooves below it ; the abapical suture coincides with the lower edge of the figure. Page 412.

Pleurotomaria glyndensis sp. nov.

FIGS. 2*a–c*. Holotype (B.M., 88804). Cenomanian, *Schloenbachia varians* Zone, Lower Chalk ; Glynde, Sussex. (*a*, *b*) Abapertural and basal views (× *c*. 1) ; (*c*) part of side of shell, viewed in a direction normal to its slope (× 3). Page 414.



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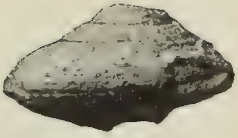

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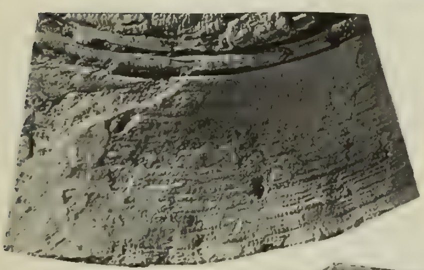

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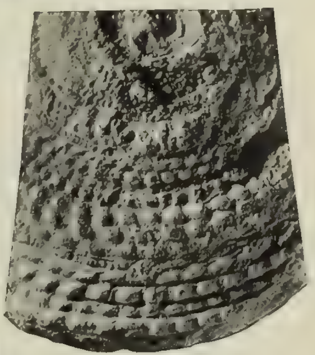

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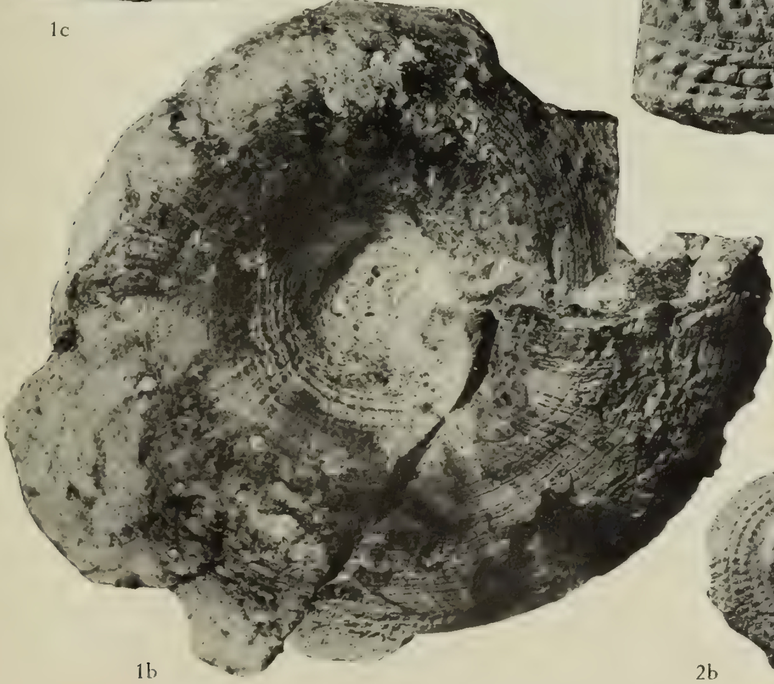
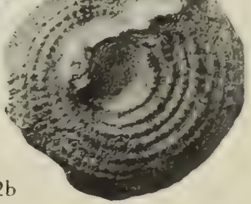


1b



2b

PLATE 54

Leptomaria seatonensis sp. nov.

Figs. 1*a b*. Holotype (B.M., G.89493). Cenomanian Limestone; Havencliff, near Seaton, Devon. (*a*) Apertural view (×1); (*b*) side of shell, viewed in a direction normal to its slope (×2·3). Page 398.

Leptomaria seatonensis sp. nov.

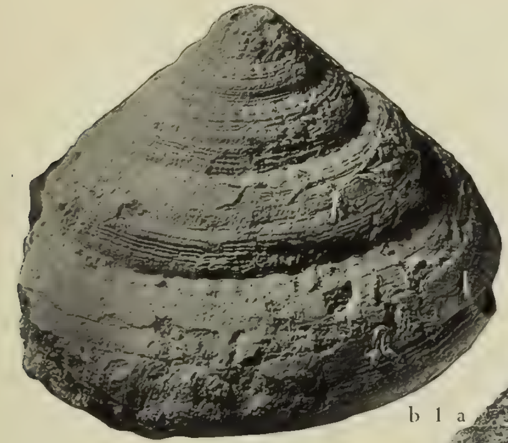
Fig. 2. Paratype (B.M., G.49914). Cenomanian Limestone; 2 miles east of Seaton, Devon. Part of side of shell, viewed in a direction normal to its slope (×3).

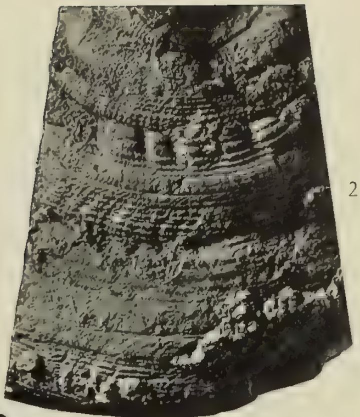
Bathrotomaria velata (Goldfuss)

Figs. 3*a–c*. (B.M., G.49923.) Cenomanian Limestone; Bindon landslip, east of Seaton, Devon. (*a*) Abapertural view (×1); (*b*) base (×1·5); (*c*) part of side of shell, viewed in a direction normal to its slope (×3); the suture is barely distinguishable, the position of its lowest appearance lying just above the middle of the figure. Page 405.

Bathrotomaria velata (Goldfuss)

Fig. 4. (S.M., B.34804.) Cenomanian, Lower Chalk; Glynde, Sussex (×1·1).





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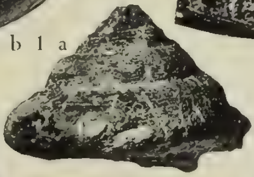

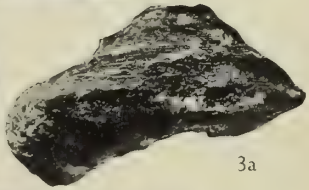

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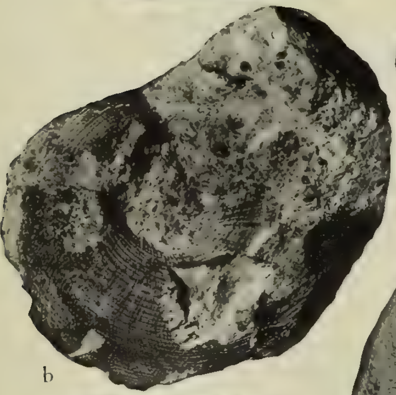
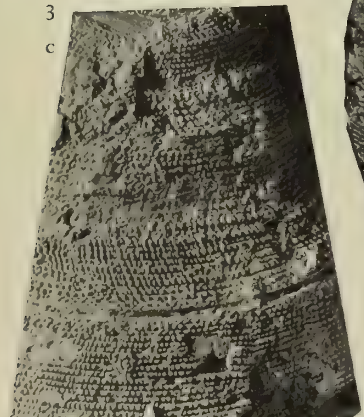
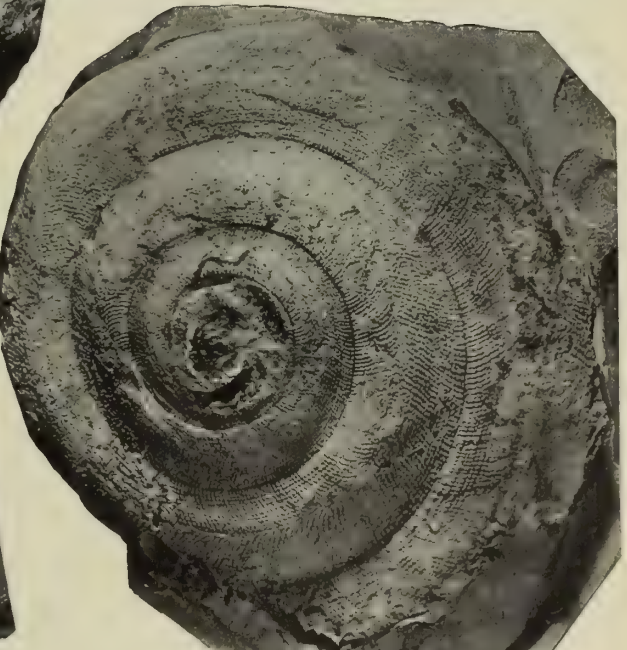


b

3

c





4

PLATE 55

Bathrotomaria dixoni sp. nov.

FIGS. 1*a–c*. Holotype (B.M., G.49898). Cenomanian Limestone ; near Culverhole, east of Seaton, Devon. (*a*, *b*) Apertural and abapertural views (×1) ; (*c*) side of shell, viewed in a direction normal to its slope (×3). Page 404.

Bathrotomaria dixoni sp. nov.

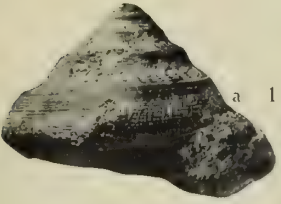
FIG. 2. Paratype (B.M., G.82347). Cenomanian, Lower Chalk ; Dover. Apical view (×1) ; the specimen has been somewhat flattened by pressure.

Bathrotomaria linearis (Mantell)

FIGS. 3*a–c*. Lectotype (B.M., 8639). Cenomanian, *Schloenbachia varians* Zone, Lower Chalk ; Hamsey, near Lewes, Sussex. (*a*, *b*) Apertural and apical views (×1·1) ; (*c*) part of side of shell, viewed in a direction normal to its slope (×2·3) ; the suture appears in a position slightly below the diamond-shaped scar towards the top of the figure and, again, meets the right-hand margin of the figure just below its middle. Page 403.

Bathrotomaria linearis (Mantell)

FIG. 4. (B.M., 88795.) Cenomanian, Lower Chalk ; near Heytesbury, Wiltshire. Apical view (×1).



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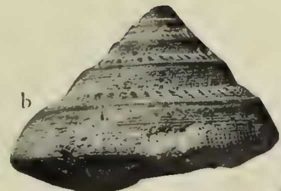

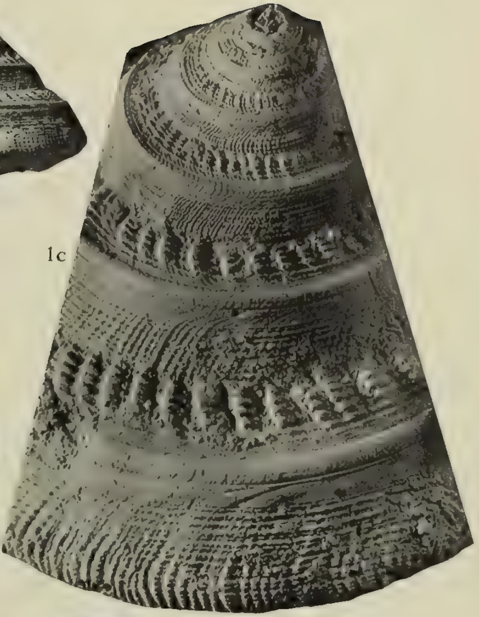

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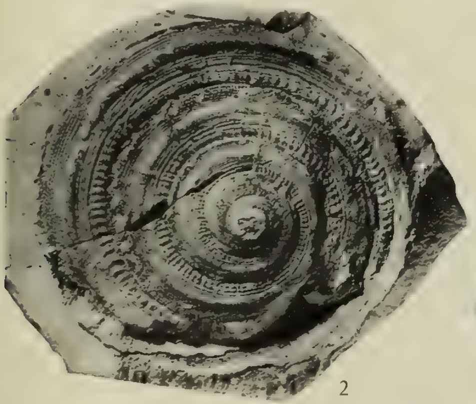

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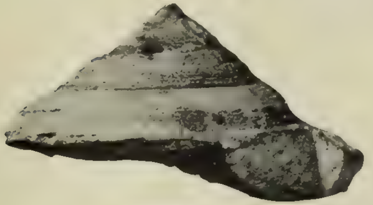
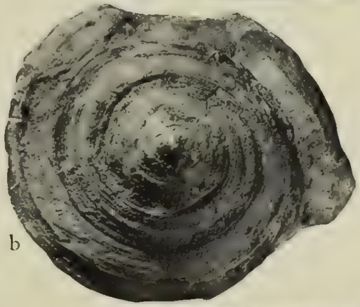
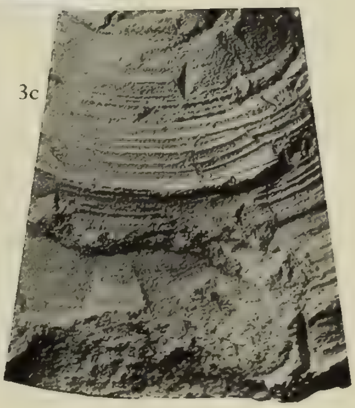




a 3 b



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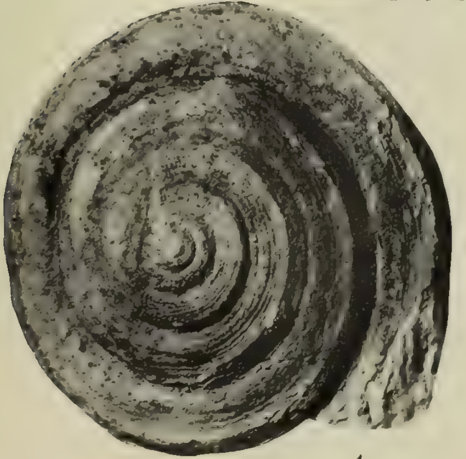


4

PLATE 56

Bathrotomaria ashburneri sp. nov.

Holotype (B.M., G.78106). Cenomanian, *Schloenbachia varians* Zone, Lower Chalk ; Chinnor, Buckinghamshire. (*a*, *b*) Basal and apertural views (× 1) ; (*c*) part of side of shell, viewed in a direction normal to its slope (× 1·5) ; the suture appears near the top of the figure and, again, slightly above the middle. Page 405.

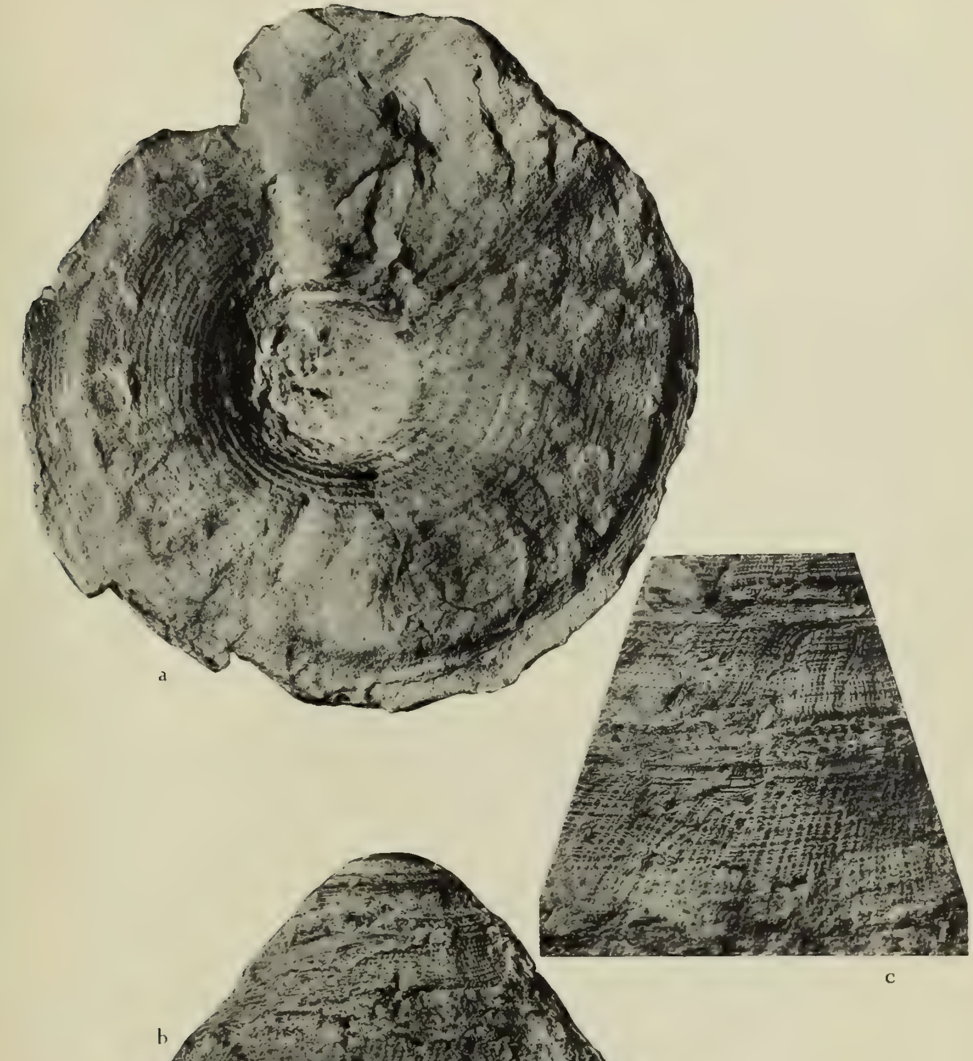

a
c
b

PLATE 57

Bathrotomaria regalis (Roemer)

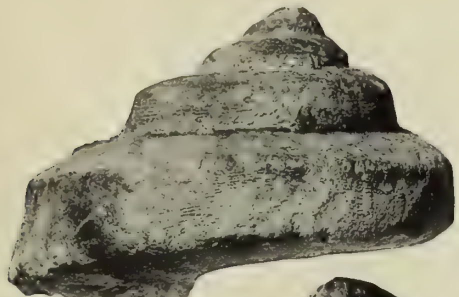
FIGS. 1*a–c*. (B.M., G.8824.) Upper Cenomanian, *Holaster subglobosus* Zone, Gray Chalk; Folkestone, Kent. Abapertural, basal and apertural views (× 1). Page 408.

Conotomaria percevali sp. nov.

FIGS. 2*a*, *b*. Holotype (B.M., G.23029). Cenomanian Limestone; near Axmouth, Devon. Apertural and basal views (× 1). Page 411.

Bathrotomaria regalis (Roemer)

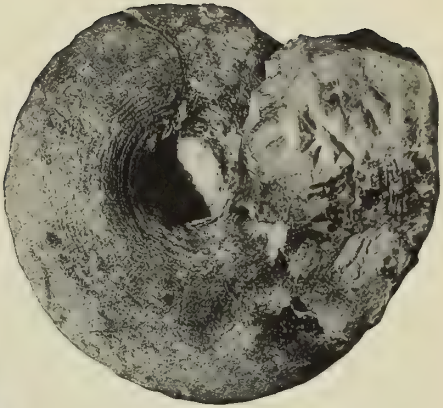
FIG. 3. (B.M., G.19058.) Upper Senonian, *Belemnitella mucronata* Zone; Magdalen Chapel, Norwich (× 1).

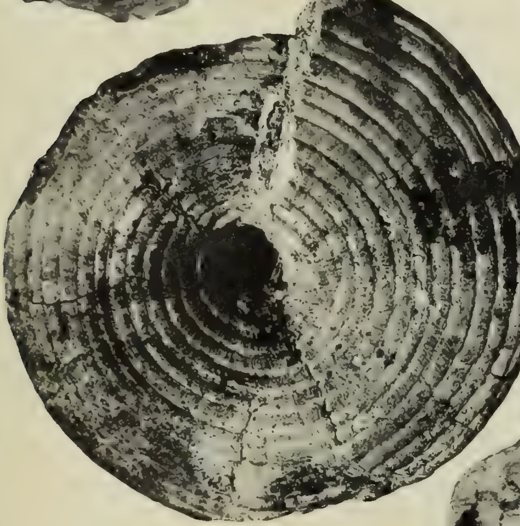


1

a

b





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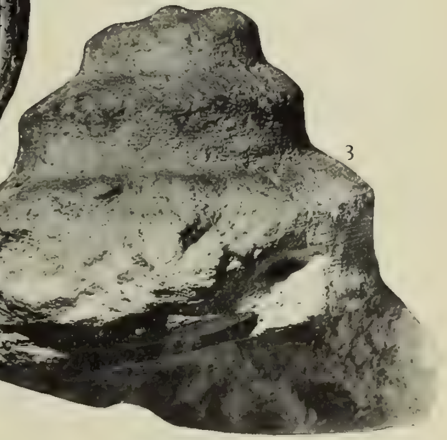

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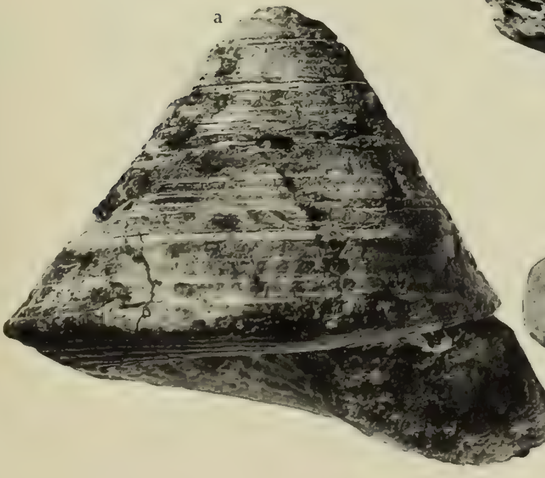
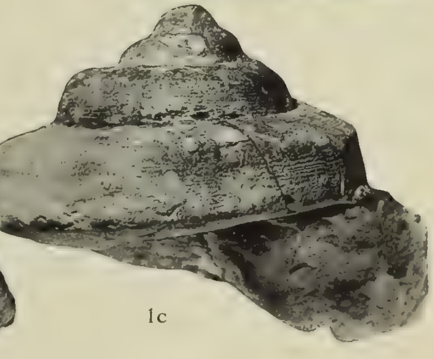




1c

PLATE 58

Bathrotomaria perspectiva (Mantell)

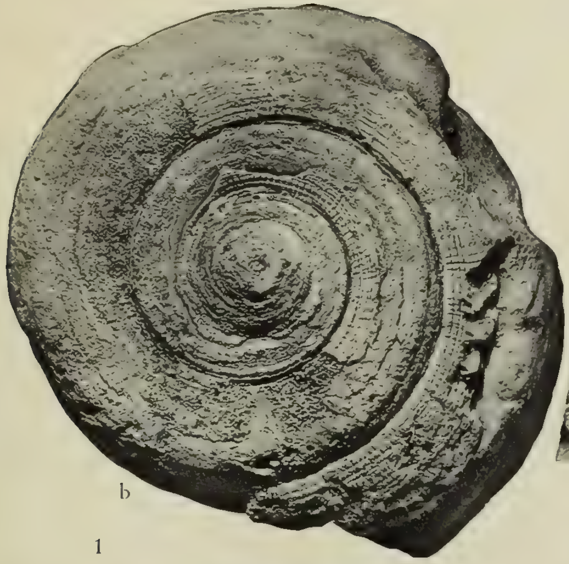
FIGS. 1*a–c*. (B.M., G.88794.) Turonian, *Holaster planus* Zone, Chalk Rock; Oldbury Hill, Wiltshire. Depressed specimen; (*a*, *b*) apertural and apical views (× 1); (*c*) part of surface of two whorls (× 2·5). Page 406.

Bathrotomaria perspectiva (Mantell)

FIG. 2. (B.M., G.29346.) Turonian, Middle Chalk; Cuxton, Kent.

Bathrotomaria perspectiva (Mantell)

FIGS. 3*a*, *b*. (S.M., B.4775.) Turonian, *Holaster planus* Zone, Chalk Rock; Cuckhamsley, Berkshire. (*a*) Apertural view (× 1); (*b*) part of side of shell, viewed in a direction normal to its slope (× 1·6).



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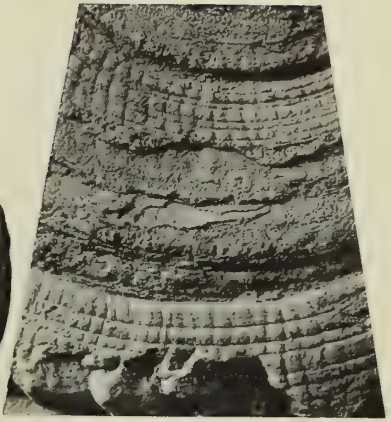

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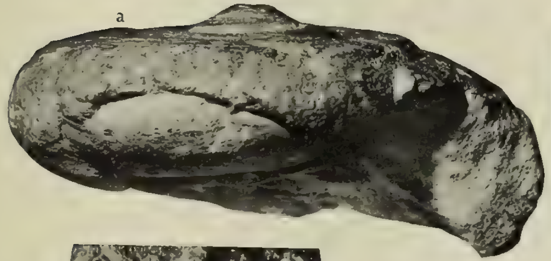

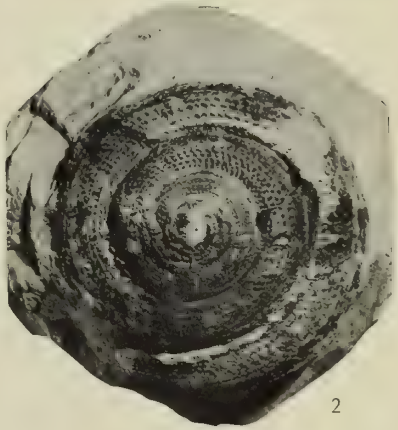

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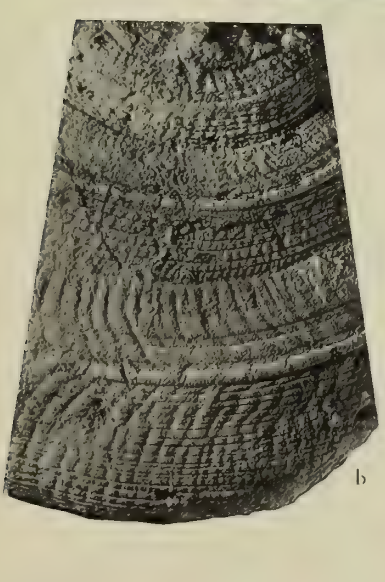

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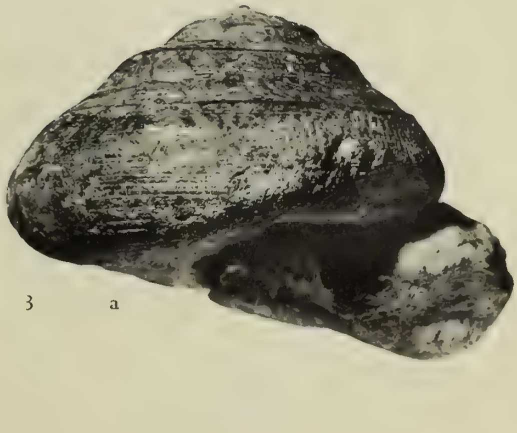


PLATE 59

Bathrotomaria perspectiva (Mantell)

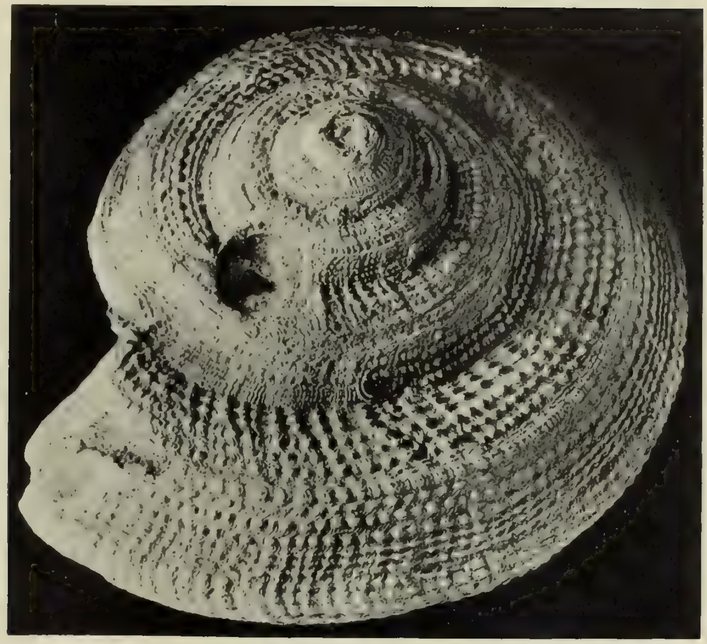
FIGS. 1*a–c*. (S.M., B.34801.) Lower Cenomanian, *Schloenbachia varians* Zone, Glauconitic Marl; Bridport, Dorset. Young specimen resembling holotype of *Cirrus granulatus* (Fig. 3) in size and ornament; (*a*, *b*) apertural and basal views (× 1); (*c*) shell viewed in a direction normal to the slope of its nearer side (× 3). Page 406.

Bathrotomaria perspectiva (Mantell)

FIG. 2. (B.M., 98208.) Cenomanian, Lower Chalk; southern England. Specimen in which the type of ornament seen in the holotype of *Cirrus granulatus* (Fig. 3) persists to late growth stages (× 1).

Bathrotomaria perspectiva (Mantell)

FIG. 3. Holotype of *Cirrus granulatus* Mantell (B.M., G.60538). Turonian ?, Middle ? Chalk; near Lewes, Sussex. Apical view (× 1); the specimen is partly crushed.



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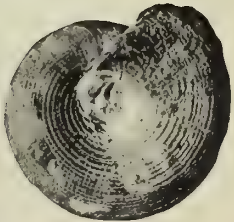

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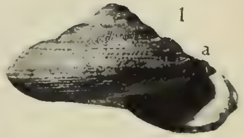

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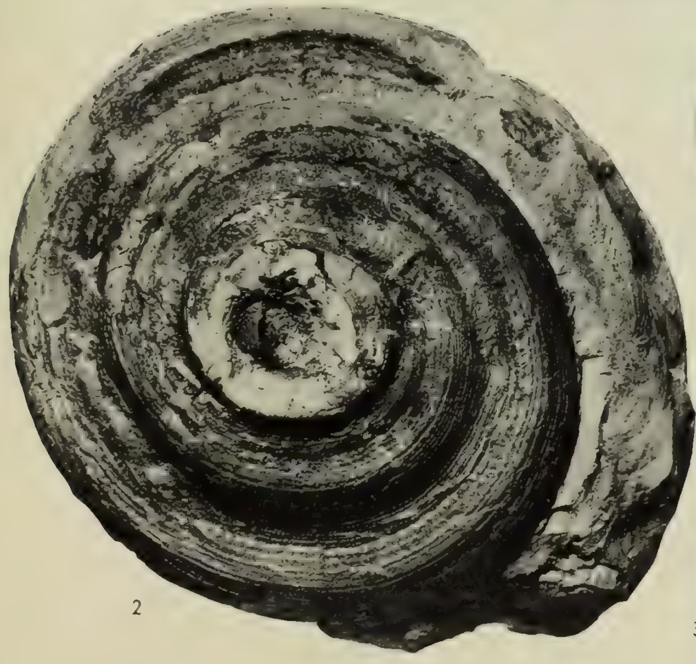

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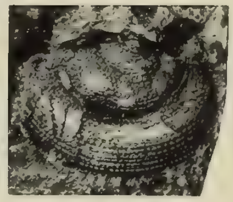

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PLATE 60

Pleurotomaria [*Conotomaria?*] I

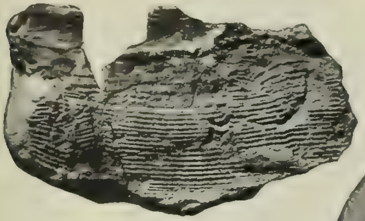
FIGS. 1*a*, *b*. (B.M., G.69750.) Senonian, *Micraster cortestudinarium* Zone; Lower, Kent. (*a*) Internal mould, side view (× 1); (*b*) attachment area of oyster shell which adhered to the gastropod and reproduces its surface ornament of spiral cords (× 1); the selenizone is best seen near the top left-hand corner. Page 418.

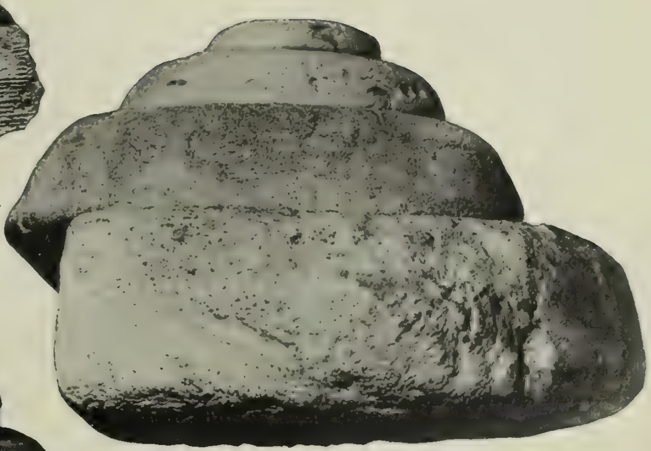
Bathrotomaria perspectiva (Mantell)

FIG. 2. (B.M., G.23040.) Turonian, *Holaster planus* Zone, Chalk Rock; near Aston Rowant, Oxfordshire. Abapertural view (× 1). Page 406.

Pleurotomaria [*Conotomaria ?*] H

FIG. 3. (B.M., G.16517.) Cenomanian; Newington, near Folkestone, Kent. Internal mould, apertural view (× 1). Page 418.





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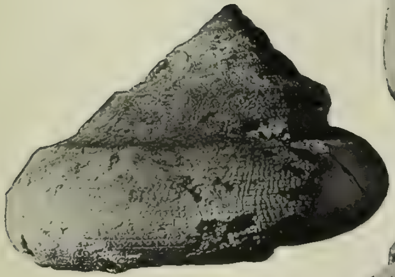

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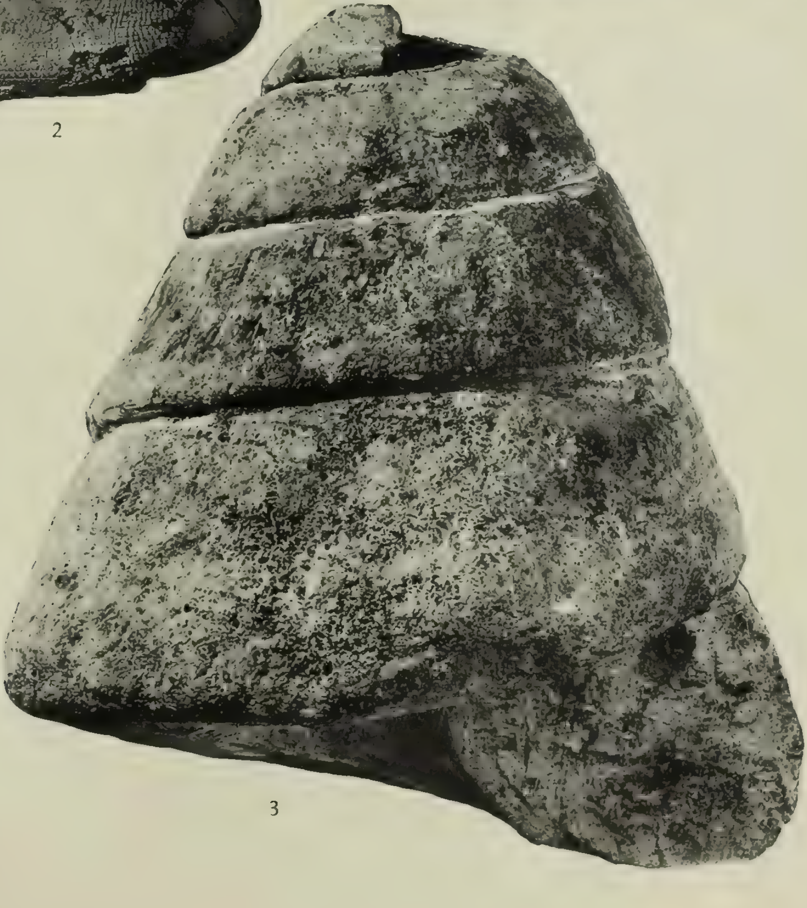

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HISTORY

TWO NEW RADIOLITIDS (RUDISTID LAMELLIBRANCHIA) FROM THE UPPER CRETACEOUS OF TURKEY

23 NOV 1960

L. R. COX

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
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BY

LESLIE REGINALD COX, F.R.S.

Pp. 425–433 ; *Pls.* 61, 62 : 1 *Text-figure*

BULLETIN OF
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TWO NEW RADIOLITIDS (RUDISTID LAMELLIBRANCHIA) FROM THE UPPER CRETACEOUS OF TURKEY

By L. R. Cox

SYNOPSIS

The species described are of late Cretaceous (Campanian or Maastrichtian) age. One, *Parasauvagesia cappadociensis* gen. et sp. nov., is made the type of a new genus thought to be derived from *Sauvagesia*; it resembles that genus in the retention of a ligamental ridge, but differs from it in having small pseudo-pillars which are, however, less complex than those of *Lapeirousia*. The second species, *Praeradiolites gordonae* sp. nov., is the largest known representative of its genus.

Rudists from the Upper Cretaceous rocks of Turkey have been described in several papers by previous authors. So long ago as 1855 S. P. Woodward based descriptions of four species of the genus *Hippurites* (*H. loftusi*, *H. colliciatus*, *H. corrugatus* and *H. vesiculosus*) on material collected by W. K. Loftus at a locality Hakim Khan [Hekimhan], about 135 km. SE. of Sivas, in central Turkey. These species, which are now known to be common throughout the country, have been re-described by Douvillé (1890–97), who examined part of the original material, preserved in the British Museum (Natural History), and by Toucas (1903–04). Böhm's (1927) monograph of a series of fossils (now in the same museum) from the Bithynian peninsula, in NW. Turkey, included descriptions of Senonian rudists referred to *Sabinia*, *Schiosia*, *Hippurites* (*H. vesiculosus* was represented), *Praeradiolites*, *Radiolites*, *Biradiolites*, and *Durania*. Among fossils from the neighbourhood of Eregli, in northern Turkey, described by Nöth (1931) were species of *Praeradiolites*, *Radiolites*, *Biradiolites*, *Sphaerulites*, and *Hippurites* (*H. vesiculosus* was again present). Stchépinsky (1941, 1942) recorded a number of rudist species from localities in northern Turkey; they included *Hippurites loftusi* and two species, *H. cornuvaccinum* Bronn and *Lapeirousia jouanneti* (Desmoulins), well known in Europe but not previously found in Turkey. Rudists from southern Turkey described by the same author in 1944 included Woodward's four hippurite species, together with *Lapeirousia jouanneti* and a remarkable form which Vautrin (1933) had found in material from northern Syria and described as *Lapeirousia syriaca*. This last form, which has proved to be widespread in the Upper Senonian of Turkey, was made the type of a new genus *Vautrinia* by Milovanović (1938: 88).[1]

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[1] Milovanović (1938: 137) also erected a new genus *Kelleria* for specimens from Syria identified by Keller (1933: 50, pl. 3, fig. 3; pl. 4, figs. 2) as *Lapeirousia jouanneti*, although he did not assign a new specific name to them. He considered their generic separation from *L. jouanneti* to be justified by their elevated, cornucopia-like form, their non-foliaceous surface bearing only strong growth-rugae, and the relatively thinner wall of their shell where it encloses the body-cavity. Stchépinsky (1944: 235), however, states that in Turkish specimens which he assigns to *L. jouanneti* the form of the lower valve ranges from depressed-conical (as in typical French specimens of the species) to high and sub-cylindrical. It would thus appear that the status of the genus *Kelleria* needs re-consideration.

In Stchépinsky's (1946) atlas of characteristic fossils of Turkey many of his previous figures of Cretaceous rudists are reproduced and others added. Reference may, finally, be made to papers by Tromp (1941) and Erentöz (1949) in which the stratigraphical distribution of some of the well-known species of *Hippurites* in Turkey is discussed. Tromp doubted if their range was as restricted as had been supposed. Erentöz considered that *H. vesiculosus* and *H. corrugatus* were good index fossils, characteristic of the Campanian rather than of the Maastrichtian, as thought by some workers, including Stchépinsky.

The present paper consists of the description of two interesting rudists, one belonging to a new genus, which have come to my notice while examining recent collections from Turkey. The type specimens of the first of these, *Parasauvagesia cappadociensis* gen. et sp. nov., were collected by geologists of the Bataafse Internationale Petroleum Maatschappij N.V. and generously presented by that Company to the Department of Palaeontology of the British Museum (Natural History). The holotype of *Praeradiolites gordonae* was collected and presented to the same museum by Miss V. Gordon, of the University of Ankara.

Family RADIOLITIDAE

Genus ***PARASAUVAGESIA*** nov.

Generic name. Intended to suggest probable affinity with *Sauvagesia* Douvillé, 1886, presumably named after the French palaeontologist H. E. Sauvage.

DIAGNOSIS.—Lower (right) valve depressed-conical, longitudinally costate, lacking growth-imbrications or readily distinguishable siphonal bands ; prismatic cells of outer layer of shell-wall with longitudinal orientation, appearing in transverse section as a polygonal network ; a short ligamental ridge and two weakly developed pseudo-pillars present ; upper (left) valve with a central elevation and a broad, more or less flattened rim ; no oscules.

TYPE SPECIES. *Parasauvagesia cappadociensis* sp. nov., Campanian or Maastrichtian, Turkey.

Parasauvagesia cappadociensis sp. nov.

(Pl. 61 ; Pl. 62, fig. 2)

Specific name. After the kingdom and later Roman province of Cappadocia, which occupied part of what is now eastern Turkey.

MATERIAL. The holotype (British Museum (Natural History), Department of Palaeontology, No. LL.10503) and one paratype (No. LL.10504).

DESCRIPTION. The lower (right) valve is very broadly conical in form and almost circular in cross-section. The holotype, the larger of the two specimens, is 80 mm. long and has a maximum diameter of 175 mm. The upper (left) valve in this specimen is hat-like in shape, with a central dome-like elevation which is about 25 mm. high and 83 mm. in maximum diameter and is surrounded by a flattened rim 40–50 mm. wide and very thin at its margin. The inner part of the rim is slightly depressed in places, but this may be a result of pressure during fossilization. The margin of the upper valve forms an unbroken curve and there is no trace of oscules. The lower valve bears numerous depressed, rounded longitudinal costae which number 3–4 to the cm. at the commissure and are separated by relatively narrow intervals. It also has very irregular growth-corrugations but no imbricating lamellae. No siphonal bands are recognizable, a narrow longitudinal depression being so irregular that it seems to be merely a surface rugosity of no significance. The upper valve is unornamented except for weak marginal corrugations.

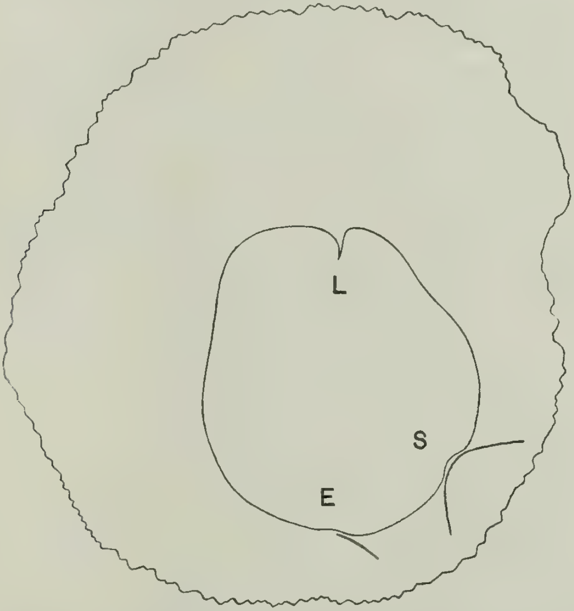

FIG. 1. *Parasauvagesia cappadociensis* gen. et sp. nov. (Brit. Mus. Palaeont. Dept. no. LL.10504). Transverse section of lower valve 15–20 mm. below commissure (× 0·75); showing ligamental ridge (L) and small pseudo-pillars marking positions of inhalant and exhalant zones (E, S). For details of structure of shell wall near S see Pl. 62, fig. 2.

In the paratype the lower valve (now sectioned) was originally about 50 mm. long and its maximum diameter at the commissure is about 155 mm. Its ornament is similar to that of the holotype. The upper valve is less perfect than in the holotype, but its central elevation can be seen to be less dome-like than in that specimen and to merge more gradually into the rim.

A transverse section of the paratype, cut 15–20 mm. below the commissure, shows a small ligamental ridge about 4 mm. long, which is curved slightly in an anterior direction and much attenuated distally, with a thorn-shaped cross-section (Text-fig. 1). Exactly opposite the ligamental ridge the wall of the shell, which is here much thinner than on the ligamental side, has a very slight inward bulge, while some distance posterior to this is a second and more marked (although by no means prominent) bulge. These bulges are similar in form and position to the so-called " pseudo-pillars " present in a number of previously described radiolitid genera, such as *Sphaerulites* and *Lapeirousia*, and it is suggested that they are of the same nature as these. According to the theory now generally accepted, they would thus mark the positions of openings in the mantle edge of the animal for the passage of inhalant and exhalant currents, or possibly of definite inhalant and exhalant siphons. As is usual in rudist descriptions, they may thus be designated (following French authors) by the letters " E " and " S " (*entrée* and *sortie*). When (as in *Lapeirousia*) oscules in the upper valve correspond to the two pseudo-pillars, some authors have suggested that the respiratory currents (or the siphons, if any existed) passed through them. In the present case, as in most radiolitids, oscules are absent and there are no gaps between the two valves when the upper one is in position. Hence respiration could have taken place and the siphons (if any) extended only when the upper valve was raised.[1]

The structure of the wall of the lower valve is clearly preserved in a number of places in the sectioned specimen. The cross-section (Pl. 62, fig. 2) shows a polygonal mesh such as is well developed in the genera *Sauvagesia* and *Durania*, the average breadth of the polygons being about 0·5 mm. On the ventral side, between the bulges " S " and " E " and on the posterior side of the former, the inner surface of the wall is lined with a series of more regular, subrectangular cells which are oriented radially, their length (in a radial direction) slightly exceeding their width. These cells are larger than those forming the polygonal mesh. Elsewhere, however, the corresponding innermost cells are of much the same size as those of the general mesh or even smaller than them. Modifications of the structure of the shell wall where the pseudo-pillars occur are indicated by the presence of a thin parabolic arc (Pl. 62, fig. 2) of denser and probably lamellose shell matter which touches the inner margin of the wall where " S " projects, and of what appears to be part of one side of a corresponding parabola located in a similar position in relation to " E ". The prismatic cells within the parabolas are mostly similar in size and arrangement to those on the rest of the wall, but near the actual bulges they become, on the average, slightly smaller.

It seems probable that certain structures visible within the body-cavity in the cross-section are accidental accumulations of crystalline calcite and not sections of teeth and myophores projecting from the upper valve. They are not, therefore, indicated in the Text-figure.

AFFINITIES. The polygonal mesh seen in the cross-section of the shell wall indicates that this radiolitid is most closely related to the group of genera (*Sauvagesia*, *Durania* and *Lapeirousia*) which Douvillé (1910 : 28) proposed to include in a " rameau " Sauvagésinés. It resembles *Sauvagesia* in the retention of a ligamental ridge, but it is distinguished from any species of that genus hitherto described by its very depressed form and by the absence of clearly differentiated siphonal bands; the presence of distinct pseudo-pillars accompanied by definite although slight modifications of the structure of the shell wall seems to justify its separation as a distinct genus. Its very depressed form and the presence of the pseudo-pillars are suggestive of *Lapeirousia*, which, together with some related genera, has been discussed in interesting papers by Milovanović (1938, 1951). In *Lapeirousia*, however, a ligamental ridge is absent except in the oldest known species, *L. aumalensis* Douvillé, the pseudo-pillars are more prominent than in the species now described, and their structure, well illustrated by Milovanović, is much more complicated.

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[1] Since it is uncertain if the radiolitids were siphonate, the term " siphonal bands ", commonly applied to longitudinal modifications (not detectable in the present species) of the exterior of the lower valve designated (for reasons just explained) as " E " and " S ", is not a happy one, but seems too firmly established to be discarded.

Douvillé (1910: 26) suggested that *Lapeirousia* was derived from *Durania*, and this view has been accepted by Moret (1936: 164–166). Wiontzek (1934: 28), however, described a supposedly ancestral genus *Praelapeirouseia*. Milovanović (1938: 131–143) has pointed out that *Lapeirousia* includes species which are more primitive in certain characters than either of the genera in question—than *Durania* in the retention of a ligamental ridge, than *Praelapeirouseia* because in that genus the pseudo-pillars have a highly specialized structure. In his view, in fact, *Lapeirousia* arose directly from *Sauvagesia*, from which the other genera just mentioned were derived independently. The new genus now described appears to have some bearing on the subject since it is intermediate between *Sauvagesia* and *Lapeirousia* in some morphological characters—the retention of a ligamental ridge combined with the presence of small pseudo-pillars and with a very depressed form. Unless, however, it is represented, by species yet to be discovered, in much older geological deposits than those (of Campanian or Maastrichtian age) in which its type species was found, it could scarcely have been an evolutionary link between those genera, since *Lapeirousia* is known to occur in strata as old as Turonian. The structure of the shell wall where the pseudo-pillars are situated differs, moreover, from that found in *Lapeirousia*, as comparison of Pl. 62, fig. 2, of the present paper with the figures of Milovanović (1938) will show. In *Lapeirousia* the cellular network behind each pseudo-pillar is interrupted by a broad arc of lamellose shell substance, the convex side of which faces towards the exterior of the shell, and between which and the outer surface there is a radial interruption of the continuity of the cellular structure of the wall. In the form now described, on the other hand, there is a thin, inward-facing arc of lamellose shell substance with no interruption of the cellular structure between it and the outer surface. The absence of oscules in the upper valve also distinguishes the present form from *Lapeirousia*.

It would thus appear that the new genus *Parasauvagesia* arose in late Cretaceous times as an offshoot from *Sauvagesia* which followed evolutionary trends towards the development of a broad, depressed shell and of pseudo-pillars which had already been pursued by *Lapeirousia* and (in the case of the pseudo-pillars) elaborated upon to a much greater extent. The retention of a ligamental ridge shows that it cannot, like *Lapeirousella* Milovanović (1938: 89, 112, pl. 4, fig, 2; pl. 5, fig. 2), be regarded as a degenerated *Lapeirousia*.

OCCURRENCE. Campanian or Maastrichtian, Zergüz, 13 km. SW. of Cermik and about 70 km. WNW. of Diyarbakir, SE. Turkey (holotype); about same horizon, Acme, 8 km. E. of Gerger and about 130 km. W. of Diyarbakir (paratype).

Genus ***PRAERADIOLITES*** Douvillé, 1903

Praeradiolites gordonae sp. nov.

(Pl. 62, figs. 1*a*, *b*)

Specific name. Named after Miss V. Gordon, of the University of Ankara, collector of the holotype.

Diagnosis. A *Praeradiolites* characterized by its large size (length over 30 cm.), its widely separated, thick, funnel-like imbricating growth-layers and its convex upper valve.

Material. The holotype only (British Museum (Natural History), Department of Palaeontology, No. LL.9568).

Description. As now preserved, the lower valve, which is acutely conical and slightly curved in a ventral direction, is about 25 cm. long ; as, however, its lower end is broken away, its original length must have well exceeded 30 cm. Its cross-section is roughly elliptical, the maximum diameter at its upper end being 10·5 cm. and its minimum (dorso-ventral) diameter 8 cm. The relatively thick outer layers of the shell imbricate upwards at irregular and, on the average, rather distant intervals, forming, as it were, a series of cones or funnels each projecting from the one below it. The upper end of each funnel, as now preserved, does not curve outwards so as to be quite out of contact with the one projecting from it, but this is probably due to the fact that the specimen is somewhat worn. For the same reason, the siphonal zones which should lie on the ventral side of the specimen are not distinguishable.

The thick upper valve, which is distinctly although not strongly convex, fits obliquely on the lower valve, sloping downwards from its dorsal side. Although its position is not clearly seen, the umbo was evidently either marginal or very close to the dorsal margin. On the ventral side the margin of this valve has two sinuses, probably indicating where the respiratory currents entered and left the pallial cavity. The sinus which on this supposition may be designated as " E " is deeper than the other one (" S ").

Remarks. This is the largest *Praeradiolites* known to me. With its well separated, funnel-like growth layers, each projecting from the one below, it much resembles *P. cylindraceus* (Desmoulins), of the Maastrichtian, and it particularly recalls a specimen of that species figured by Toucas (1907, pl. 7, fig. 7). *P. cylindraceus*, however, has a flat upper valve without marginal sinuses and with a central nucleus which does not project as a distinct umbo. The upper valve of the form now described is more like that of the Santonian species *Praeradiolites plicatus* (Lajard, Négrel & Toulouzan), but in that form the imbricating funnel-like layers of the lower valve are more closely arranged.

Occurrence. Campanian or Maastrichtian (associated with *Hippurites* (*Vaccinites*) *loftusi* Woodward), Inali Bogaz, 17 km. from Kalecik on road to Cankiri, and about 60 km. ENE. of Ankara, Turkey.

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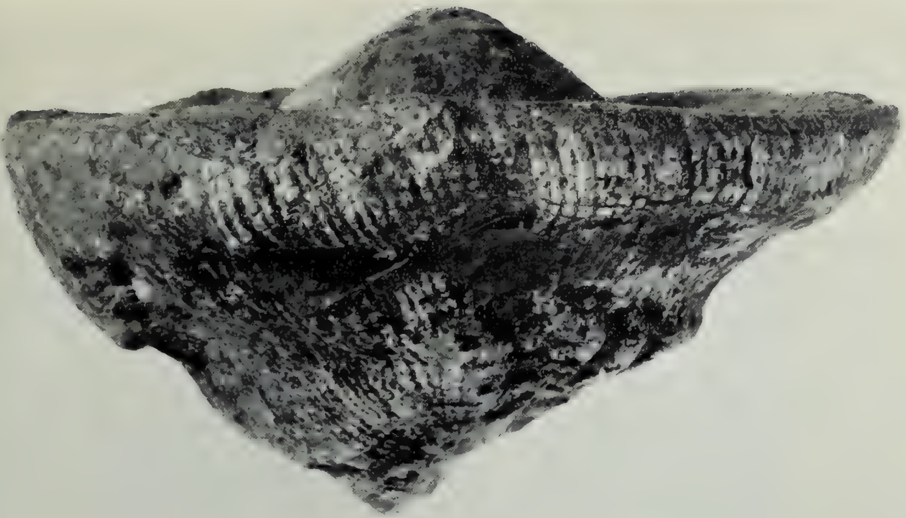
PLATE 61

Parasauvagesia cappadociensis gen. et sp. nov. Holotype (Brit. Mus. Palaeont. Dept. No. LL.10503). Side and top views (× 0·65).



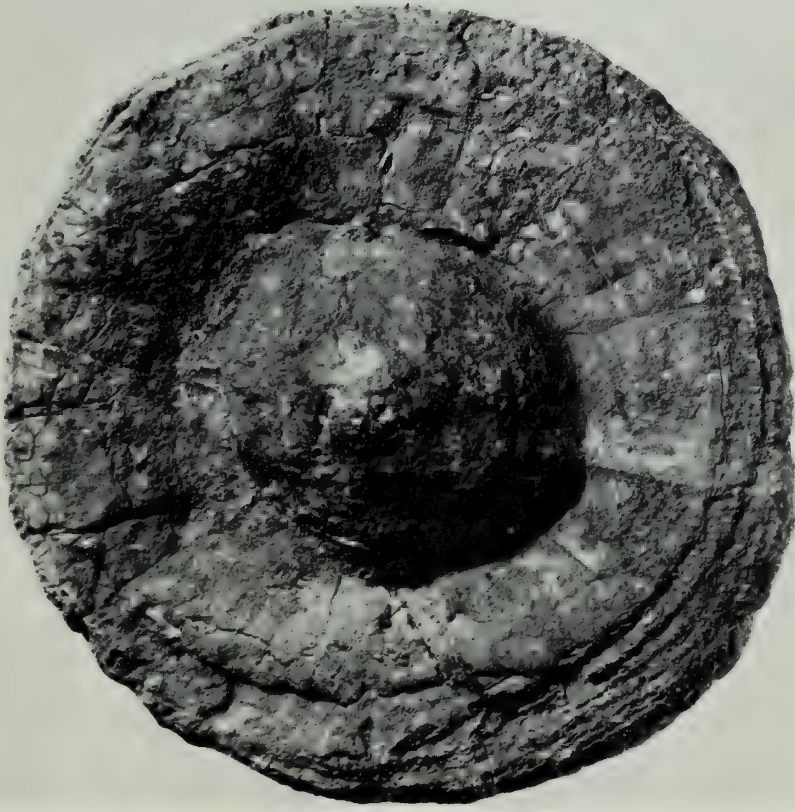
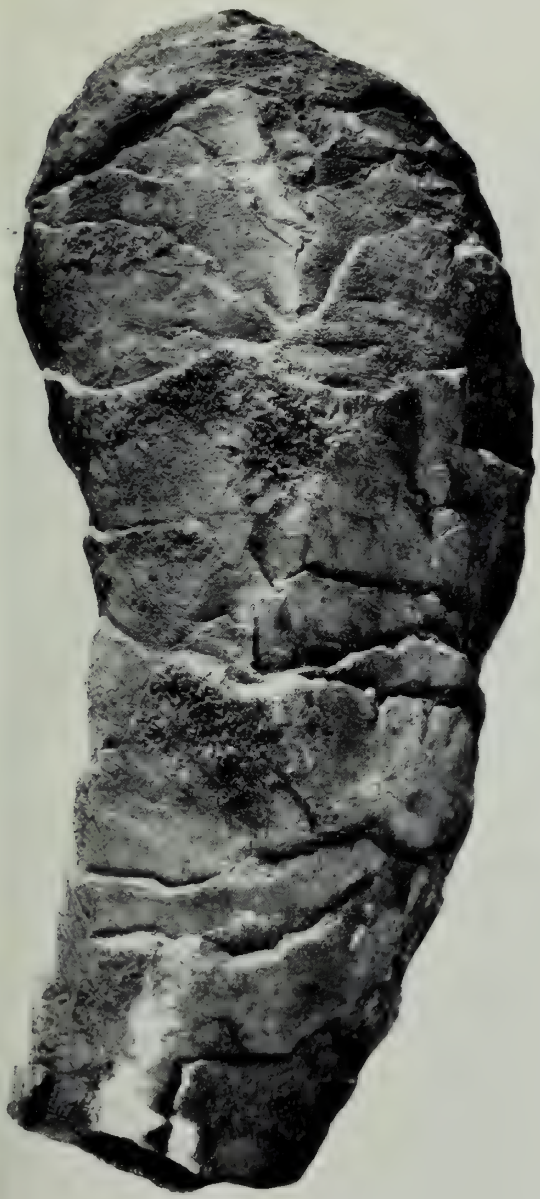


PLATE 62

FIGS. 1*a*, *b*. *Praeradiolites gordonae* sp. nov. Holotype (Brit. Mus. Palaeont. Dept. No. LL.9568). (*a*) Dorsal view of entire specimen ; (*b*) anterior view of upper part of specimen, showing convexity and tilt of upper valve (× 0·65).

FIG. 2. *Parasauvagesia cappadociensis* gen. et sp. nov. Paratype (Brit. Mus. Palaeont. Dept. No. LL.10504). Part of transverse section of lower valve, 15–20 mm. below commissure, showing polygonal mesh and pseudo-pillar " S " (× 3).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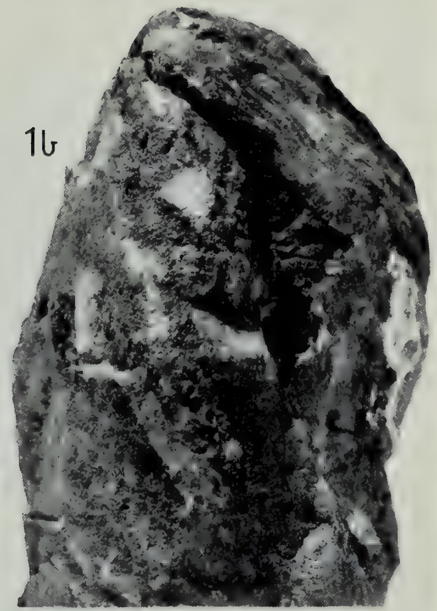
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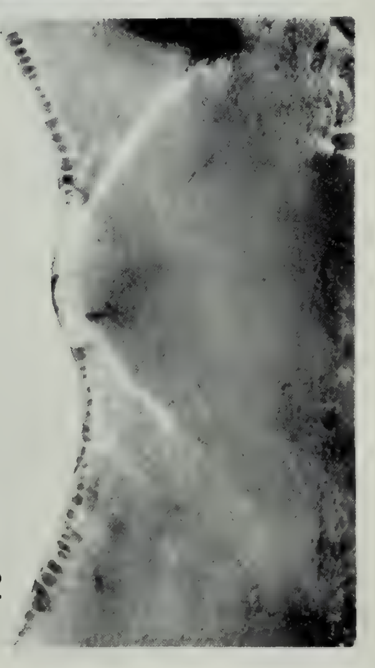
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THE LIASSIC AMMONITE ZONES AND SUBZONES OF THE NORTH-WEST EUROPEAN PROVINCE

W. T. DEAN, D. T. DONOVAN
AND M. K. HOWARTH

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BY

WILLIAM THORNTON DEAN, DESMOND THOMAS DONOVAN
AND MICHAEL KINGSLEY HOWARTH

Pp. 435–505 ; *Plates* 63–75

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THE LIASSIC AMMONITE ZONES AND SUBZONES OF THE NORTH-WEST EUROPEAN PROVINCE

By W. T. DEAN, D. T. DONOVAN & M. K. HOWARTH

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SYNOPSIS

The paper presents a scheme of ammonite zones and subzones for the Lias of Europe which lies to the north and west of the Alpine belt. It is a revision and amplification of the scheme put forward by Spath in 1942. With a few exceptions selection of the zone and subzone indices is based on priority of usage within the province. Of the 20 zones and 49 subzones used, those newly proposed are the Subzones of *Beaniceras luridum*, *Coroniceras reynesi* and *Schlotheimia extranodosa*. Two main features of the paper are a re-classification of the Hettangian into three zones instead of two as usually accepted, and the replacement of the large and unwieldly Jurense Zone of the Toarcian by three smaller zones ; both result in more balanced arrangements that are more in keeping with the ammonite sequences. Full lists and synonymies are given of all previously proposed Liassic stratal divisions based on ammonites, and the index species of each accepted zone and subzone is figured in the plates.

I. INTRODUCTION

The Table of Liassic zones and subzones published by Spath (1942) was the first attempt to standardize a set of subzones for the Lias ; the zones into which they were grouped were principally those of Oppel, the originator of Jurassic zoning. The purpose of the present paper is to revise and amplify Spath's scheme after eighteen years of use.

Spath's paper, published in war time, did not include the reason for his selection of indices, although it is clear that he worked on the basis of priority. He had written a " lengthy account of the history and delimitation of the Ammonite zones of the Lias " which was never published. We have tried to remedy the deficiency by giving authors and dates of accepted and rejected zones, and data to assist the recognition of the zones and identification of the index fossils.

In 1942 (p. 267) Spath stated that "... an ideal zonal table should be capable of being used by workers in any part of the world, and only then will lead to a more uniform terminology ". Experience has shown, however, that very few zonal indices have a world-wide distribution, and a more realistic view was taken by Arkell (1946 : 10) : " A stage is an artificial concept transferable to all countries and continents ; but a zone is an empirical unit. If the zone index species and its associated fauna are absent we cannot record the zone ... a zonal table must have specific reference to a particular area ". In spite of Spath's professed views, his Table (unlike that of Muller (1941) which Arkell was criticizing) was founded only on successions in North-west Europe, principally Britain and Germany, although this was not explicitly stated. Donovan (1957 : 147–148, 155–156) has discussed Spath's views on correlation by ammonites.

The revised zonal scheme now presented refers to a particular area : Europe north of and excluding the Alpine belt and the Pyrenees (see Pl. 75). In the Alps and country to the south the system cannot be used on account of the absence or rarity of many of the index species, apart from the question of the relative time ranges of ammonite species in the two provinces (see Donovan, 1958 : 50). A separate zonal system is necessary there ; this has been worked out for the Toarcian (Donovan, 1958), but for earlier stages stratigraphical information is not yet adequate.

The paper has been written as follows :

Hettangian to Lower Pliensbachian—D. T. D.
Upper Pliensbachian and Toarcian (Whitbian)—M. K. H.
Toarcian (Yeovilian)—W. T. D.

II. INTERPRETATION OF ZONE AND SUBZONE

The subject and its terminology have been fully discussed by Arkell (1933 : 14–35). There has never been complete agreement as to the interpretation and usage of stratigraphical units, as is shown by the recent exchange of views between Arkell (1956*a*, 1958) and Schindewolf (1957). In the scheme here presented, the units are the subzones, which often correspond to the range of a genus, subgenus or species. For instance, the Raricostatum Subzone corresponds to the range of the genus *Echioceras*, the Conybeari Subzone to that of the subgenus *Metophioceras*, and the Subnodosus Subzone to the range of its index species *Amaltheus subnodosus*. The zones were originally defined by their index species and by other characteristic ammonites ; in most cases these have since been found to be restricted to certain parts of the zone, which is now most satisfactorily defined in terms of the included subzones. It is doubtful whether a single zonal index species in the Lias ranges throughout the whole of the zone to which it gives its name. In some cases zones can be defined in terms of the ranges of genera : the Spinatum Zone corresponds to the range of the genus *Pleuroceras*, and the Angulata Zone to that of *Schlotheimia*. In these cases, the zone can sometimes be recognized when fossils are too poorly preserved or too fragmentary for the subzone to be identified.

III. PRINCIPLES FOLLOWED IN ZONAL NOMENCLATURE

We have tried to follow the simple rules suggested by Arkell (1946 : 3). We add to these the principle that zonal and subzonal indices should be co-ordinate with one another (in the language of Zoological Nomenclature) ; that is, an index first used for a subzone has priority from this usage if it is upgraded to a zone, and vice versa. Zones are dated from the earliest usage except when this was clearly wrong, when the fact is commented on (see Johnstoni and Scipionianum Subzones).

The only one of Arkell's rules which we feel to be disputable is that dealing with zonal indices which prove to have been misidentified by the original user (rule 4) ; Arkell proposed to use these with their correct names but with priority from the original introduction (with wrong name). This rule could result in the replacement of familiar indices by new names : for instance, Belcheri Subzone (not in fact used) might be held to have priority over Portlocki Subzone (Lang, 1924), by those who believe that von Schloenbach's Johnstoni Zone (1863) was founded on *Ammonites belcheri* (see pp. 444–445). Such cases are few and we prefer to solve each on its own merits.

The priority rule is qualified in so far as it is restricted to the province for which the Table is intended. For instance, the Marmorea Zone, first used in the eastern Alps (see p. 446) is not considered available, although its index species occurs in North-west Europe. Transference of zones from one province to another will only lead to confusion and is to be avoided.

We have not been able to pursue a consistent policy with regard to the double use of a species as both zonal and subzonal index (Spath, 1942 : 266). Double use is probably better avoided, but a satisfactory alternative cannot always be found. Spath's double use of Angulata disappears as a result of the reclassification of the Hettangian, but Bucklandi and Oxynotum remain in double use, and Raricostatum, Jamesoni, Falcifer and Levesquei are added.

IV. HEMERAE

Hemerae are briefly mentioned, although by definition they are not synonymous or interchangeable with zones. We do not accept priority of zonal indices from previous use as hemerae, but such use sometimes influenced the naming of zones and not all workers were careful to maintain the distinction between zones and hemerae. The introduction of hemeral indices for the Lias dates from 1898, many of those then published being equivalent to zones as now recognized (Buckman, 1898 : Table facing p. 450). In subsequent works Buckman and other authors employed a large number of additional hemerae. Many are to be found in Buckman (1918 ; 1925), and a table showing Buckman's final scheme will be found in the last volume of *Type Ammonites* (Buckman, 1930 : 37–47). It should be emphasized that the majority of hemerae were hypothetical chronological units and were not defined stratigraphically.

V. LIMITS OF THE NORTH-WEST EUROPEAN LIASSIC AMMONITE PROVINCE

The extent of the province is shown in Pl. 75, the southern and eastern parts of the boundary being marked by the heavy dashed line. To the south and south-east lies the Mediterranean Liassic Ammonite Province, which includes the outcrops of the Lias in Portugal, Spain, North Africa and Italy, and the Pyrenees and Alpine belt ; knowledge of Lias ammonites from further east is not sufficient to enable the eastern boundary of this province to be determined. The North-west European Province should probably include the Lias outcrops in southern Sweden, for the ammonites appear to belong to north-west European species, but knowledge of their stratigraphical distribution is lacking.

VI. TABLE OF STAGES, SUBSTAGES, ZONES AND SUBZONES

Stage	Substage	Zone	Subzone
Toarcian	Upper Toarcian or Yeovilian	*Dumortieria levesquei*	*Pleydellia aalensis*
			Dumortieria moorei
			Dumortieria levesquei
			Phlyseogrammoceras dispansum
		Grammoceras thouarsense	*Pseudogrammoceras struckmanni*
			Grammoceras striatulum
		Haugia variabilis	
	Lower Toarcian or Whitbian	*Hildoceras bifrons*	*Zugodactylites braunianus*
			Peronoceras fibulatum
			Dactylioceras commune
		Harpoceras falcifer	*Harpoceras falcifer*
			Harpoceras exaratum
		Dactylioceras tenuicostatum	
Pliensbachian	Upper Pliensbachian or Domerian	*Pleuroceras spinatum*	*Pleuroceras hawskerense*
			Pleuroceras apyrenum
		Amaltheus margaritatus	*Amaltheus gibbosus*
			Amaltheus subnodosus
			Amaltheus stokesi
	Lower Pliensbachian or Carixian	*Prodactylioceras davoei*	*Oistoceras figulinum*
			Androgynoceras capricornus
			Androgynoceras maculatum
		Tragophylloceras ibex	*Beaniceras luridum*
			Acanthopleuroceras valdani
			Tropidoceras masseanum
		Uptonia jamesoni	*Uptonia jamesoni*
			Platypleuroceras brevispina
			Polymorphites polymorphus
			Phricodoceras taylori
Sinemurian	Upper Sinemurian	*Echioceras raricostatum*	*Paltechioceras aplanatum*
			Leptechioceras macdonnelli
			Echioceras raricostatum
			Crucilobiceras densinodulum
		Oxynoticeras oxynotum	*Oxynoticeras oxynotum*
			Oxynoticeras simpsoni
		Asteroceras obtusum	*Eparietites denotatus*
			Asteroceras stellare
			Asteroceras obtusum
	Lower Sinemurian	*Caenisites turneri*	*Microderoceras birchi*
			Caenisites brooki
		Arnioceras semicostatum	*Euagassiceras sauzeanum*
			Agassiceras scipionianum
			Coroniceras reynesi
		Arietites bucklandi	*Arietites bucklandi*
			Coroniceras rotiforme
			Coroniceras (*Metophioceras*) *conybeari*

Stage	Substage	Zone	Subzone
Hettangian	—	*Schlotheimia angulata*	*Schlotheimia complanata*
			Schlotheimia extranodosa
		Alsatites liasicus	*Alsatites laqueus*
			Schlotheimia (*Waehneroceras*) *portlocki*
		Psiloceras planorbis	*Psiloceras* (*Caloceras*) *johnstoni*
			Psiloceras planorbis

VII. THE STAGES, ZONES AND SUBZONES

Under the heading INDEX SPECIES references are given to the original description, and to authors who have refigured or revised the species. An example of the index species to each zone and subzone is figured in the plates, in many cases from type material.

The heading NOMENCLATURE refers to stratigraphical nomenclature; here the first use of each unit is stated, followed by subsequent changes in meaning, and synonyms.

Under the heading STRATIGRAPHY criteria useful for recognizing the unit are noted, together with brief details of its development and geographical extent.

HETTANGIAN STAGE

This stage was introduced by Renevier (1864 : 86) for Oppel's Planorbis and Angulata Zones. At the type-locality of Hettange (Moselle), France, ammonites are rare in the Grès d'Hettange but this formation is overlain by limestones and shales containing early Bucklandi Zone ammonites and it may therefore be correlated with the Hettangian Stage as usually understood.

The term Infralias, first used by Leymerie (1838 : 376) in a sense equivalent to Hettangian, later became extended to include rocks of Rhaetian age below. The rejection of the term Infralias was favoured by Renevier when he proposed the Hettangian Stage.

Buckman's Caloceratan Age (1898 : 446) was defined as " time of Hettangian Stage ". It was later replaced (1925) by Psiloceratan and Schlotheimian Ages.

Spath (1942) retained Oppel's two zones, each with two subzones, as follows, and indicated a number of horizons said to be of local value :

Zones	Subzones	Horizons
Scamnoceras angulatum	*Scamnoceras angulatum* (s.s.)	*Schlotheimia complanata*
		S. lymense
		S. phoenix
	Alsatites laqueus	*Saxoceras gallicum*
		S. prometheus
		Psilophyllites hagenowi
Psiloceras planorbis	*Caloceras johnstoni*	*Waehneroceras portlocki*
		C. johnstoni (s.s.)
	P. planorbis (s.s.)	

This scheme is unsatisfactory for several reasons : the subzone of *C. johnstoni* includes the horizon of *W. portlocki*, but a series of faunas dominated by *Waehneroceras* continues into the subzone of *A. laqueus*. The zone of *S. angulatum* is extended downwards to include the latter subzone. Both the zones are unwieldy.

A more balanced scheme comprises three zones, giving separate recognition to the *Waehneroceras-Alsatites* faunas. The Planorbis Zone will then correspond nearly to the range of *Psiloceras* and the Angulata Zone to that of *Schlotheimia*. This arrangement was first employed by Collenot (1869 : 64), and adopted by Haug (1910 : 954) and many other continental authors.

PLANORBIS ZONE

(Pl. 63, fig. 1)

INDEX SPECIES. *Psiloceras planorbis* (J. de C. Sowerby, 1824 : 69, pl. 448). Lectotype designated and figured by Arkell (1956 : 760, pl. 31, fig. 7).

NOMENCLATURE. First used by Oppel (1856 : 24). Synonyms : Burgundiae Zone (Zone à *Amm. Burgundiae*) of Martin (1860 : 28) ; Psilonotus Zone (Vaughan & Tutcher, 1903 : 10, 12, 14).

STRATIGRAPHY. Oppel cited *Ammonites planorbis* and *Ammonites johnstoni* J. de C. Sowerby as guide fossils for the zone, and it has since been found that they characterize successive levels throughout the province. The zone is therefore divided into two subzones on this basis.

Planorbis Subzone

(Pl. 63, fig. 1)

INDEX SPECIES. As for Planorbis Zone.

NOMENCLATURE. See Planorbis Zone. A subzone of Planorbis *s.s.* was first employed by Trueman (1922 : 251). The Psilonotum Zone as used by North German authors is equivalent to Planorbis Subzone. Includes the *planorbis, aequabile, erugatum, psilonotus* and *plicatus* hemerae (Buckman, 1930 : 47).

STRATIGRAPHY. Subdivision of this part of the sequence has not been convincingly accomplished and Buckman's five hemerae (see above) are at least partly hypothetical (Donovan, 1952 : 635). There is evidence for distinguishing a lower horizon with smooth species of *Psiloceras* s.s. (*P. planorbis, P. psilonotum* (Quenstedt)) from an upper with plicate ones (*P. plicatulum* (Quenstedt)) near Bristol, England (Donovan, 1952 : 634), and in the Psilonotenbank of South Germany (Frank, 1931 : 11) ; this sequence is not yet proved to be generally valid. The subzone is almost universally present throughout the province, but is said to be absent in the Pfälz area of westernmost Germany (Jüngst, 1938 : 154).

In Britain there are in many areas a few feet of strata without ammonites at the base of the Blue Lias, underlying rocks with the Planorbis Subzone fauna. The name Pre-Planorbis Beds has often been applied to them, and species of lamellibranchs have been used as zonal indices, viz. *Ostrea liassica* Strickland and *Pteromya crow-*

combeia Moore, the latter superseded by *Pleuromya tatei* Richardson & Tutcher. Details will be found in the forthcoming Jurassic section of the Lexique Stratigraphique International for Britain.

Donovan (1956 : 198) pointed out that the first appearance of ammonites does not necessarily mark a constant horizon and proposed that the Planorbis Subzone be extended downwards to include the old " pre-Planorbis Beds ", the lamellibranch zones being retained, for local use only, if needed.

Johnstoni Subzone

(Pl. 63, fig. 2)

INDEX SPECIES. *Psiloceras* (*Caloceras*) *johnstoni* (J. de C. Sowerby, 1824 : 70, pl. 449, fig. 1).

NOMENCLATURE. A zone of *Ammonites johnstoni* was first used by von Schloenbach (1863 : 498), as the equivalent in North Germany of the Planorbis Zone, but later research has shown that the ammonites previously known as *Caloceras johnstoni* in North Germany do not belong to that species (Hoffmann, 1949 : 114).[1]

According to Arkell's proposed rules (1946 : 3, Rule 4) this should become the Belcheri Zone with priority from von Schloenbach. The Johnstoni Subzone as correctly used may be taken to date from Stoddart (1868 : 201 : Johnstoni-beds) or Tutcher (1918 : 279 : Johnstoni Zone). It was made the upper subzone of the Planorbis Zone by Trueman (1922 : 251). It is equivalent to Buckman's *johnstoni* hemera (1930 : 47).

STRATIGRAPHY. The base of the subzone is marked by the appearance of *Caloceras*, *P*. (*C*). *johnstoni* being probably the earliest species. The genus ranges up into the Portlocki Subzone with species such as *P*. (*C*). *belcheri* (Simpson) and *P*. (*C*.) *bloomfieldense* Donovan. The top of the subzone is taken at the appearance of *Waehneroceras*. The subzone as here understood is smaller than the Johnstoni Subzone of Spath (1942), which included the strata here separated as the Portlocki Subzone. The subzone is absent or unproved in North Germany, as remarked above, but is present in Britain and France. The index fossil is recorded from South Germany but this identification awaits confirmation.

LIASICUS ZONE

(Pl. 63, fig. 3)

INDEX SPECIES. *Alsatites liasicus* (d'Orbigny, 1844 : 199, pl. 48). The lectotype was designated by Donovan (1952 : 644) and figured by Reynès (1879, pl. 6, figs. 9–12).

NOMENCLATURE. First used by Collenot (1869 : 64) who inserted it between the Planorbis and Angulata Zones. It has priority over Laqueus Zone (Reynès, 1879), here retained as a subzone. Spath was evidently unaware of the earlier publication of Liasicus, for he believed (unpublished MS.) Laqueus to have priority. *Alsatites laqueolus* (Schloenbach), used as a zonal index by Hoffmann (1949 : 114), is a synonym of *A. liasicus* (see Donovan, 1952 : 644). The Catenatum Subzone provisionally proposed by Quilter (1886 : 65) is also a synonym of Liasicus Zone.

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[1] Lange (1941) and Hoffmann (1949) identify them as *C. torus* (d'Orbigny) ; in the present writer's view they are *C. belcheri* Simpson (see Donovan, 1952 : 637).

STRATIGRAPHY. The zone is best defined in terms of its two subzones, for the range of *Alsatites liasicus* is not well established. The more detailed subdivision of the lower part, which has been used in some areas, is reviewed under the Portlocki Subzone. Lang's (1924 : 181) Zone of *Alsatites liasicus* on the Dorset coast is a much smaller unit which falls at the top of the zone as it is here understood.

Portlocki Subzone

(Pl. 63, fig. 4)

INDEX SPECIES. *Schlotheimia* (*Waehneroceras*) *portlocki* (Wright, 1881, pl. 48, figs. 4, 5). See Donovan (1952 : 646).

NOMENCLATURE. Introduced by Lang (1924 : 172, 182), in a more restricted sense than now used. For general use the subzone includes the Hagenowi Zone of Lang (1924), and the Torus, Schroederi and Angersbachense Zones of Lange (1931 : 352) although these may be useful for local successions (see below). The Megastoma Zone of Waehner (1886 : 169) is a senior synonym even if accepted only from its adoption for the British sequence by Buckman (1910*a* : xvi). It was proposed, however, for the east-Alpine area and is not considered available for the province now under consideration.

The Longipontinus Zone of Oppel (1862 : 92 ; 1863 : 131) was proposed as a substitute for the Planorbis and Angulata Zones together. If restricted to the range of the index species, *Schlotheimia* (*Waehneroceras*) *longipontina* (Oppel), it might be held to be a prior name for Portlocki Subzone. It is not now adopted because it has not been employed since its introduction, and the index species has not been commonly recorded from the province.

Includes the *portlocki* and *hagenowi* hemerae of Buckman (1930 : 47).

STRATIGRAPHY. The base of the subzone is taken at the first appearance of *Waehneroceras*. *Alsatites* may first appear in the subzone in some areas. Locally the beds included in the subzone have been further divided, as many as four subdivisions being recognized in North Germany (Lange, 1931 : 352, α 1b–e). The lowest is the *torus* horizon (*recte* Belcheri " Zone ", see above) which has not been recorded elsewhere, but is presumably represented by the beds which yield *Psiloceras* (*Caloceras*) *belcheri* (Simpson) in Yorkshire ; their stratigraphy is inadequately known. The next, the *hagenowi* horizon, has been identified at a number of places : the Pfälz area of western Germany (Jüngst, 1938, fig. 3) ; south-western Germany (Frank, 1931 : 14, etc.) ; Dorset, England (Lang, 1924 : 182) ; and Glamorgan, Wales (Trueman, 1920). It is not certain, however, whether all these occurrences lie at a constant horizon, and on account of this fact, the sporadic occurrence of the index species, and the difficulty of identifying it[1] (possibly a reason for the apparently sporadic distribution) the horizon is not adopted for general use. The two highest subdivisions are said to be characterized by *Saxoceras schroederi* Lange and S. *angersbachense* Lange, which, in the present writer's opinion, are species of *Waehneroceras* allied to *W. portlocki*. In most areas the fossil material is not good enough for the sequence of *Waehneroceras* species to be elucidated, and so these horizons cannot be used generally.

Laqueus Subzone

(Pl. 63, fig. 5)

Index species. *Alsatites laqueus* (Quenstedt, 1856 : 43, pl. 3, fig. 5). See Donovan (1952 : 642).

Nomenclature. First used in the explanations to plates 2 and 3 of Reynès' Atlas (1879). Spath (1942) adopted the index for the lower subzone of his Angulata Zone. Lange's Costatum Zone (1931 : 352) is a synonym. Buckman's *gallica*, *prometheus*, *laqueus* and *megastoma* hemerae correspond to the subzone (1930 : 47).

Stratigraphy. The subzone is recognizable throughout the province. *Waehneroceras* may range up into it, and the boundary with the Portlocki Subzone is taken at the first appearance of the index species or of the genus *Saxoceras* which is characteristic of the subzone.

ANGULATA ZONE

(Pl. 64, fig. 5)

Index species. *Schlotheimia angulata* (Schlotheim, 1820 : 70). Lectotype designated and figured by Lange (1951 : 33, pl. 1, fig. 2).

Nomenclature. First used by Oppel (1856 : 28). The Marmorea Zone of Waehner (1886 : 169–170), used by Buckman as a hemera (1898, Table facing p. 450), and as a zone (1910*a* : xvi), is a synonym as far as the present province is concerned, although a valid zone for the east Alpine area ; the index species is a *Charmasseiceras* (Donovan, 1952 : 653) and is not confined to the Angulata Zone. The Moreanus Zone of Martin (1860 : 38) is a synonym, and was said by Martin to be the equivalent of the Angulata Zone.

Buckman's *acuticosta*, *angulata*, *marmorea* and *phoenix* hemerae correspond to the zone (1930 : 47).

Stratigraphy. The base of the zone is marked by the incoming of *Schlotheimia* (s.s.), and the top by the appearance of *Coroniceras* (*Metophioceras*). The latter horizon may not be constant but a better criterion cannot be suggested at present. The zone as now interpreted is equivalent to Angulata Subzone of Spath (1942). It is not easy to recognize subzones of general usefulness. Three are recognized in North Germany, but only two are provisionally adopted here.

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[1] *Psilophyllites hagenowi* has the same shell-form as *Psiloceras*, and is distinguished only by the septal suture. There are transitional species (" *Neophyllites* " of Lange, 1941).

Extranodosa Subzone

(Pl. 64, fig. 1)

Index species. *Schlotheimia extranodosa* (Waehner, 1886 : 168, pl. 20, figs. 10, 11). See Donovan (1952 : 651).

Nomenclature. The name replaces Germanica Zone of Lange (1922 : 461–462) whose index species was a *nomen nudum* when the zone was introduced, and on description (Lange, 1924 : 201 ; 1951 : 69, pl. 8, fig. 11) proved to be synonymous with *S. extranodosa* (Donovan, 1952).

Stratigraphy. The subzone is well developed in North Germany, and is represented in southern England by the index species (Donovan, 1956 : 186). The sucession within the Angulata Zone in France is insufficiently known. In North Germany a zone of *Schlotheimia amblygonia* Lange is recognized below the Extranodosa (" Germanica ") Subzone, within the Angulata Zone ; it has not been distinguished elsewhere.

Complanata Subzone

(Pl. 64, fig. 2)

Index species. *Schlotheimia complanata* von Koenen (1902 : 9, pl. 7, figs. 4–6). Type refigured by Lange (1925, pl. 21, figs. 5*a*, *b*).

Nomenclature. The name replaces Stenorhyncha Zone of Lange (1922 : 461, 463). When first used the index species *Schlotheimia stenorhyncha* was a *nomen nudum*, but it was described by Lange (1924 : 202) and figured in 1951 (pl. 15, figs. 1*a*, *b*). Spath (1942 : 267) suggested a *complanata* horizon to replace Lange's *stenorhyncha*, then still unfigured. In the present writer's view the two species are synonyms.

Stratigraphy. This subzone forms the highest subdivision of the Angulata Zone in North Germany but is only locally developed (Lange, 1922 : 463). In southern England the subzone is represented by beds with *Schlotheimia similis* Spath, closely related to the index species, in Dorset (Lang, 1924 : 181) and Somerset (Donovan, 1956 : 201, etc.). In southern England the beds with *S. similis* are succeeded by strata with giant species (*S. pseudomoreana* Spath) but palaeontological data are inadequate, and the beds have not been traced elsewhere, although they may be represented by Jüngst's (1938 : 154, 163) " Unnamed zone " with large Schlotheimiidae above the " Stenorhyncha " Zone in the Pfälz area of western Germany.

SINEMURIAN STAGE

The division into zones is unchanged from that of Spath (1942), with a few changes to subzones and consequent slight alterations in zonal boundaries. The zones date from Oppel, except that the upper part of his Bucklandi Zone has been separated as the Semicostatum Zone, and his zone of *Pentacrinus tuberculatus* has been replaced by an ammonite zone, the Turneri Zone. The division into Lower and Upper Sinemurian was first made by Oppel (1856 : 59) who spoke of Obtusum, Oxynotum and Raricostatum Zones as constituting the Upper Sinemurian.

The Lotharingian Stage of Haug (1910 : 948) was used for the Turneri (also called Birchi, p. 964), Obtusum, Oxynotum and Raricostatum Zones, the last two being used as alternatives by Haug. Lotharingian was erroneously equated with Upper Sinemurian in Oppel's sense by Spath (1942). Certain French authors have used the Lower Sinemurian for the Bucklandi and Semicostatum Zones only, thus making the Upper Sinemurian larger and equivalent to Lotharingian (e.g. Gignoux, 1950 : 352), while others (e.g. Abrard, 1948 : 12) follow Haug (1910) in restricting Sinemurian to these two zones. Buckman (1910*a* : xvi) excluded the Raricostatum Zone from the Sinemurian and placed it at the base of the Charmouthian Stage.

The Sinemurian as here understood includes four stages introduced by Buckman (1917 ; 1918 : 267–275) : Lymian, Mercian, Deiran and Raasayan. Having been defined in terms of a hypothetical hemeral system their limits are not well established. Lymian corresponds to the Bucklandi and Semicostatum Zones, but includes a *birchi* hemera at the top. Since the *brooki* and *turneri* hemerae were excluded it cannot be synonymous with Lower Sinemurian, although it was so equated by Spath (1942 : 265). Mercian corresponds approximately to the Turneri and Obtusum Zones, and Raasayan includes the Raricostatum Zone. These terms are not adopted in this paper.

The Sinemurian from the base up to the Oxynotum Zone inclusive corresponds to the Asteroceratan Age of Buckman (1898 : 447), later restricted by the separation of Vermiceratan, Coroniceratan, Agassiceratan, Microderoceratan and Oxynoticeratan Ages. Buckman's Deroceratan Age, as later restricted, corresponds approximately to the Raricostatum Zone but includes the base of the Jamesoni Zone.

BUCKLANDI ZONE

(Pl. 64, fig. 3)

Index species. *Arietites bucklandi* (J. Sowerby, 1816 : 69, pl. 130). See Donovan (1952 : 718). The neotype was figured by Arkell (1956, pl. 31, fig. 4).

Nomenclature. Introduced by Oppel (1856 : 35), and later restricted by the proposal of the Semicostatum Zone (see p. 451).

Stratigraphy. The two lower subzones reflect an evolutionary trend in the genus *Coroniceras* and are well established, but stratigraphy of the upper part of the zone is less satisfactory. *Vermiceras scylla* (Reynès) is found in the Conybeari and Rotiforme Subzones, and the Schlotheimiidae *Charmasseiceras* occurs throughout the zone.

Conybeari Subzone

(Pl. 64, fig. 4)

Index species. *Coroniceras* (*Metophioceras*) *conybeari* (J. Sowerby, 1816 : 70, pl. 131). See Donovan (1952 : 728).

Nomenclature. First used, as a zone, by Tutcher (1918 : 279). Trueman (1922 : 251) placed it as the lowest subzone of the Bucklandi Zone. Spath (1924 : 187) included in the Conybeari Zone two hemerae, *longidomus* and *brevidorsale*, on the basis of records of these species from Württemburg. Hoffmann (1949 : 114) adopted *Vermiceras longidomus* as a zonal index for the lowest zone of the Sinemurian, and as *Coroniceras* (*Metophioceras*) *longidomum* (Quenstedt) the index was used for south-western Germany by Walliser (1956 : 217). Longidomum Zone is a synonym of Conybeari Subzone as here used.

The subzone includes the *longidomus*, *brevidorsale* and *scylla* hemerae (Buckman, 1930 : 47). The *charmassei* hemera was placed by Buckman (1925 : 78) above his *bucklandi* hemera, but it probably falls in this or in the next subzone.

STRATIGRAPHY. There is general agreement that the appearance of the subgenus *Metophioceras* marks the base of the Sinemurian. It has been recorded throughout the province, with the exception of north-western Germany, where there is a non-sequence at this level (Hoffmann, 1949 : 114). Further subdivision does not seem practical. Spath's hemerae mentioned above were adopted by Muller (1941, Table 2) as subdivisions, of unspecified rank, of the Conybeari Subzone. According to Walliser (1956 : 197, 216), who states that the two species are closely allied, their ranges overlap, but *Coroniceras* (*Metophioceras*) *longidomum* (Quenstedt) appears first and *C.* (*M.*) *brevidorsale* (Quenstedt) survives later. There is no evidence yet that this succession is of more than local importance.

Rotiforme Subzone

(Pl. 65, fig. 2)

INDEX SPECIES. *Coroniceras rotiforme* (J. de C. Sowerby, 1824 : 76, pl. 453). See Donovan (1952 : 730).

NOMENCLATURE. *Ammonites rotiformis* was first used as a zonal index by Collenot (1879 : 790), replacing his earlier and incorrect use of *Am. scipionianus* above Angulatus and below Bucklandi (1869 : 132). Trueman (1922 : 251) reduced the zone to the status of a subzone of the Bucklandi Zone. Fiege (1926 : 210) spoke of a " Zone of *Arietites Schloenbachi* " which is probably synonymous with Rotiforme Subzone. He stated that *Coroniceras westfalicum* Lange was identical with *C. schloenbachi* (Reynès), but later Hoffmann (1949 : 114) employed these two species as indices for successive zones, presumably with special reference to Germany. The subzone includes the *kridion*, *rotator* and *schloenbachi* hemerae (Buckman, 1925 : 78 ; 1930 : 47).

STRATIGRAPHY. The subzone succeeds the Conybeari Subzone throughout the province, the lower boundary being marked by the incoming of *Coroniceras* (s.s.). The upper boundary is not so satisfactory, but is conveniently drawn immediately below the appearance of large ammonites of the genera *Arietites* and *Pararnioceras* : the matter is discussed below (Bucklandi Subzone). Locally the subzone can be divided but it does not seem possible to correlate the subdivisions in England and Germany. In southern England *Coroniceras rotiforme* and allied species, such as *C. schloenbachi* (Reynès), are confined to the lower part of the subzone, while the upper part is characterized by *Coroniceras caprotinum* (d'Orbigny) and *C. hyatti* Donovan,[1] as demonstrated by Donovan (1956 : 207, 210–211) and confirmed by the

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[1] This group is referred to as *Arnioceratoides* in the publications of Spath and Trueman.

Stowell Park Borehole (Spath, 1956 : 157). In Germany *Coroniceras westfalicum* is stated to be earlier than *C. schloenbachi*, as noted above, but a separate *C. caprotinum* horizon has not been distinguished. *Coroniceras caprotinum* is found in Württemberg, as shown by the series of examples from Vaihingen figured by Reynès (see Donovan, 1955 : 27). The latest work on the South-west German Lias (Walliser, 1956) does not distinguish any subdivisions of the Rotiforme Subzone. In France, in the type area of the Sinemurian (the Semur area, Côte d'Or), the horizon with *C. rotiforme* is succeeded by one characterized by *C. kridion*,[1] recalling the succession in southern England. The *C. kridion* fauna is already accompanied by *Pararnioceras meridionale* (Reynès) (Mouterde, 1953 : 396).

Bucklandi Subzone

(Pl. 64, fig. 3)

Index species. See Bucklandi Zone.

Nomenclature. See Bucklandi Zone. After the separation of the Semicostatum Zone, the zone was further restricted by the introduction of the Rotiforme Zone. In 1942 Spath reduced this restricted zone to the status of a subzone of the Bucklandi Zone.

The subzone includes the *bucklandi* hemera of Buckman (1930 : 46) and probably the *charmassei* hemera of Spath (1924).

Stratigraphy. It is often difficult to delimit the subzone for the index species is seldom common, and has often been misinterpreted. Like *Pararnioceras meridionale* (Reynès), which also occurs in the subzone, it is a large ammonite and is rarely collected *in situ*. Its stratigraphical position has been confirmed in the Bristol Region (Donovan, 1956 : 203). Certainly in Britain, and probably throughout the province, *Arietites bucklandi*[2] is not a good subzonal index fossil, but nothing better can yet be suggested. There should be no hesitation in abandoning it if a better species is forthcoming.

In the Stowell Park Borehole Spath (1956 : 160) noted three distinct divisions of the subzone, but they cannot be correlated with sections elsewhere. The ammonites referred by Spath to his genus *Epammonites* (probably merely closely ribbed species of *Coroniceras* (*Primarietites*)) are found in the subzone. The remaining noteworthy feature of the subzone is the first appearance of the genus *Arnioceras*.

SEMICOSTATUM ZONE

(Pl. 65, fig. 4)

Index species. *Arnioceras semicostatum* (Young & Bird, 1828 : 257, 359). The holotype was refigured by Buckman (1918*a*, pl. 112) and again by Jaworski (1931, pl. 5, figs. 1*a*, *b*).

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[1] *Coroniceras kridion* (Hehl MS. *in* Zieten), the type of which has recently been refigured by Walliser (1956, pl. 10, fig. 5) is apparently the inner whorls of a species of the *hyatti-caprotinum* group. It is not the inner whorls of *C. rotiforme*.

[2] As properly restricted ; in the past it was often used as all-embracing name for large, bisulcate arietitids.

Nomenclature. The zone was proposed by Judd (1875 : 42) to replace the Geometricus Zone used by Oppel for the upper part of his comprehensive Bucklandi Zone. Oppel's *Ammonites geometricus* (1856 : 79) was a homonym of *Ammonites geometricus* Phillips (1829), and as such was rejected by Spath (1942 : 266) as a zonal index. Lang's Arnioceras Zone (1914 : 312) is a synonym.

Stratigraphy. The existing subzones, adopted by Spath (1942) from Tutcher (1918), are retained except that Gmuendense is replaced by Reynesi Subzone (see below). The genus *Arnioceras* itself is of little stratigraphical use : it has a long range, up to a horizon high in the Obtusum Zone, and although Spath (1956 : 161) has given a succession of species, the fact remains that species from the Obtusum Zone (e.g. *A. semicostatoides* Spath) are barely distinguishable from *A. semicostatum*, unless exceptionally well-preserved material is available (Spath, 1956 : 151). The zone is retained, in default of a better alternative, but the presence of the index fossil, without supporting ammonites, cannot be taken as positive evidence for its identification.

In consequence of the abandonment of the Alcinoë Subzone the boundary between the Semicostatum and Turneri Zones is placed higher than by Spath (1942), at the incoming of *Caenisites* instead of at the disappearance of *Euagassiceras*.

Reynesi Subzone

(Pl. 65, fig. 5)

Index species. *Coroniceras reynesi* (Spath, 1923 : 72). Lectotype figured by Reynès (1879, pl. 24, figs. 27, 28) and designated by Donovan (1952 : 738).

Nomenclature. The subzone is here proposed to replace the Gmuendense Zone introduced by Buckman (1910*a* : xvi), and adopted by Spath (1942) as the lowest subzone of the Semicostatum Zone. *Ammonites gmuendensis* Oppel was described but never figured by its author, and Prof. Dehm, of Munich, informs me (*in litt.*) that no type material can now be recognized. Numerous figures purporting to represent the species have been published but they include several species, and Spath's selection (1922 : 173) of Reynès' figures was irregular. As the species cannot be defined it cannot be used as a zonal index.

The *gmuendense*, *meridionalis* and *vercingetorix* hemerae (Buckman, 1918 : 274 ; 1930 : 46) fall in the subzone.

Stratigraphy. In Somerset *Coroniceras reynesi* is abundant in the beds above the Bucklandi Subzone, which also yield occasional examples of *Paracoroniceras*, that is, species related to *C. reynesi* in which the outer whorl acquires a trigonal section. The species occurs in Germany (the syntypes ; compare also the ammonites figured by Fiege (1929) as *Arietites bucklandi*) but precise stratigraphical information is lacking. In France data are also insufficient ; it is possible that Mouterde's horizon of *Arnioceras ceratitoides* (1953 : 396–397) represents this subzone.

Scipionianum Subzone

(Pl. 65, fig. 3)

INDEX SPECIES. *Agassiceras scipionianum* (d'Orbigny, 1844 : 207, pl. 51, figs. 7–8). See Donovan (1952 : 745).

NOMENCLATURE. The subzone as correctly understood dates from Tutcher (1918 : 279) who used it as a zone, but it was reduced to the status of a subzone by Trueman (1922 : 251). A zone of *Ammonites scipionianus* had been used by Collenot (1869 : 132), but he placed it too low, between his Angulatus and Bucklandi Zones. Junior synonyms are the Pseudokridion Zone (Lang, 1924 : 176), Acuticarinatum Zone (Spath, 1924 : 186), and Colesi Subzone (Muller, 1941, Table 2). The subzone includes the *Agassiceras* hemera of Buckman (1918 : 274), and the *acuticarinatum, colesi* and *pseudokridion* hemerae of Spath (1924 : 187).

STRATIGRAPHY. Besides the index species the subzone is characterized by *Arnioceras acuticarinatum* (Simpson) and the genus *Metarnioceras*. On the Dorset coast and in the Stowell Park Borehole *M. pseudokridion* Spath occurs just above *A. scipionanum* and Lang (1924 : 176) recognized a separate Pseudokridion Zone. This may be useful for southern England but confirmation of its general validity is lacking. In Auxois *Metarnioceras pellati* (Dumortier) is recorded above *Euagassiceras sauzeanum* (Mouterde, 1953 : 227). The subzone is present throughout the province; in Württemberg, according to Walliser (1956 : 216) *Paracoroniceras* ("*Arietites gmuendensis*") survives into it, and the index fossil is accompanied by the large *Agassiceras nodosaries* (Quenstedt).

Sauzeanum Subzone

(Pl. 65, fig. 1)

INDEX SPECIES. *Euagassiceras sauzeanum* (d'Orbigny, 1844 : 304, pl. 95, figs. 4, 5). D'Orbigny's figured specimen was refigured by Hyatt (1889, pl. 6, figs. 12, 13). The index species is probably a synonym of *E. resupinatum* (Simpson, 1843 : 15) but not figured until much later (Buckman, 1909, pl. 6). See Donovan (1952 : 742),

NOMENCLATURE. The Sauzeanum Zone of Tutcher (1918 : 279) was reduced to the status of a subzone of the Bucklandi Zone by Trueman (1922 : 251) and transferred to the Semicostatum Zone by Spath (1942). It is now extended to include the Alcinoë Subzone of Muller (1941, Table 2) (see below), and also embraces Muller's Striaries and Gaudryi Subzones. It includes the *alcinoë*, *Euagassiceras*, *sauzeanum* and *striaries* hemerae of Spath (1924 : 187) and Buckman (1930 : 46).

STRATIGRAPHY. The subzone is recognized throughout the province. It is characterized by various species of *Euagassiceras* but some of these, although not, apparently, *E. sauzeanum* itself, first appear in the Scipionianum Subzone.[1]

In 1942 Spath adopted the Alcinoë Subzone from Muller (1941), who derived it from the *Pararnioceras alcinoë* Bed in Dorset (Lang, 1923 : 61). Since the horizon of this fossil has not been recognized elsewhere, except in the Stowell Park Borehole, it is discarded as a subzonal index. The *P. alcinoë* horizon in southern England is now included in the Sauzeanum Subzone, for *Euagassiceras* persists into it in Dorset.

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[1] Walliser's Table (1956 : 216) shows *sauzeanum* appearing in the succession before *scipionianum*; but reference to p. 202 of his paper shows that he includes in *E. sauzeanum* the species *E. spinaries* (Quenstedt) which is present in the Scipionianum Subzone in Dorset. See also Hallam (1960 : 3, 4).

TURNERI ZONE

(Pl. 66, fig. 2)

INDEX SPECIES. *Caenisites turneri* (J. de C. Sowerby, 1824 : 75, pl. 452). The lectotype was designated by Buckman (1898 : 453) and refigured by Wright (1879, pl. 12, fig. 4).

NOMENCLATURE. The zone was introduced by Wright (1860 : 403) to replace Oppel's Zone of *Pentacrinus tuberculatus*. Muller (1941, Table 2), who applied the name Semicostatum Zone to this part of the sequence (see Spath, 1942), divided it into Alcinoë, Nodulosum, Sulcifer, Brooki, Hartmanni and Birchi Subzones. It is difficult to place these in the synonymy of the subzones now accepted, since they were derived from Buckman's hemerae (1930 : 46) of the same names, the order of which was hypothetical. Buckman's *ploti*, *inflatum*, *turneri* and *turgescens* hemerae also fall within the zone (1930 : 45, 46).

STRATIGRAPHY. The zone is now divided into two subzones only, Spath's Alcinoë Subzone at the base having been incorporated in the Sauzeanum Subzone (see above). The subzones are not widely applicable and may have to be abandoned or replaced. A subzonal scheme founded on species either of *Microderoceras* or of *Caenisites* alone would be preferable, but does not seem to be feasible on present evidence.

Brooki Subzone

(Pl. 66, fig. 1)

INDEX SPECIES. *Caenisites brooki* (J. Sowerby, 1818 : 203, pl. 190).

NOMENCLATURE. The subzone was introduced by Lang (1914 : 317) as a subdivision of Oppel's Obtusum Zone in the Dorset coast succession, but the stratigraphical position of the index species was misunderstood. This was rectified later (Lang, 1923) and the subzone transferred to the Turneri Zone by Spath (1942).

STRATIGRAPHY. In Dorset the index species is restricted to one three-inch bed (Lang, 1923 : 59) and the only satisfactory way to define the subzone is by additional species of *Caenisites*. The base of the subzone is characterized by *C. preplotti* Spath and *C. costariformis* Spath and the top by *C. brooki*. There seem to be no good supporting species of other genera. In Dorset " *Sulciferites* " is restricted to the lower part of the subzone, but in the Stowell Park Borehole it was found in the Birchi Subzone (Spath, 1956 : 152) ; as the " genus " differs from *Charmasseiceras* of the Bucklandi Zone merely by its later date, examples may be expected at intermediate horizons. In view of these considerations and of the difficulty of distinguishing between species of *Caenisites* the subzone is not a satisfactory one, and it has not been generally recognized on the Continent. It is retained in the hope that further evidence as to the position of *Caenisites*, and the appearance of *Microderoceras* in continental countries, may be forthcoming.

Birchi Subzone

(Pl. 66, fig. 3)

Index species. *Microderoceras birchi* (J. Sowerby, 1820 : 121, pl. 267).

Nomenclature. The zone was first used by Collenot (1869 : 132) for the Auxois district of France, and has been generally adopted. Spath (1942) used it as a subzone of the Turneri Zone. The Capricornoides Zone of Lang (1936 : 160) is a synonym.

Stratigraphy. The range of the index species at its type locality, on the Dorset coast, is small (Lang, 1923 : 57–58), but the subzone has been generally interpreted as corresponding to the vertical range of *Microderoceras*. *Caenisites* persists into the subzone, while the upper part is characterized by *Promicroceras capricornoides* (Quenstedt). The top of the subzone is taken at the appearance of the genus *Asteroceras* at the base of the Obtusum Zone. The Capricornoides Zone in northern Germany, with *Microderoceras birchi* and *Promicroceras capricornoides* (Hoffmann, 1944 : 289), is presumably the exact equivalent of the Birchi Subzone in Britain. On the north side of the Massif Central ammonites are too scarce at this level for detailed subdivision (Mouterde, 1953 : 404). In the Stowell Park Borehole, Spath (1956 : 144) placed a subzone of " *birchi-turneri* " below one of " *capricornoides* ", but *M. birchi* persists into the upper subzone (p. 152). Further evidence is needed before this sequence can be regarded as generally valid.

In southern Germany Walliser (1956 : 216–217) records *M. birchi* already in the Scipionianum Subzone. As some of the other species dealt with in his paper are interpreted widely, it is uncertain whether or not this record refers to *M. birchi* as strictly interpreted. It is clear, however, from this and other evidence, that *Microderoceras* may be found as low as the Semicostatum Zone, and that care is necessary in the use of the Birchi Subzone. It may be that the general non-recognition of the Brooki Subzone is due to earlier appearance of *M. birchi* in some regions.

OBTUSUM ZONE

(Pl. 67, fig. 1)

Index species. *Asteroceras obtusum* (J. Sowerby, 1817 : 151, pl. 167 upper figure (lectotype, selected by Spath, 1925 : 300)).

Nomenclature. The zone was introduced by Oppel (1856 : 50).

It includes the *obtusum*, *sagittarium*, *planicosta*, *stellare* and *denotatus* hemerae of Buckman (1930 : 45).

Stratigraphy. In addition to *Asteroceras* the zone is characterized by the Asteroceratinae *Aegasteroceras* and *Epophioceras*, both of sporadic occurrence, and in the upper part by *Eparietites*. The accompanying Eoderoceratidae are *Promicroceras* and *Xipheroceras* but their species seem to be of less value for stratigraphical subdivision than the Asteroceratinae. The last species of *Arnioceras* are found in the zone. The division into the Obtusum, Stellare and Denotatus Subzones, long accepted in England, reflects an evolutionary trend in the Asteroceratinae towards increasing compression of the whorls and reduction of the size of the umbilicus. The subzones have not been widely recognized on the Continent.

Obtusum Subzone

(Pl. 67, fig. 1)

Index species. See Obtusum Zone.

Nomenclature. In 1926 Lang used an " Obtusum Zone " in a very restricted sense, for a small part only of the Obtusum Zone of Oppel (see above). In 1942 Spath returned to the original use (approximately) of the Obtusum Zone, and he included a subzone of " *Promicroceras planicosta* or *obtusum* s.s." In 1956 (p. 150) he rejected *planicosta* in favour of *obtusum* as the subzonal index. The Planicosta Zone of Lang (1914 : 317, 319) is therefore a synonym. Dumortier's " Couches à *Ammonites planicosta* " (1867 : 95), however, are equivalent to the Raricostatum Zone.

Stratigraphy. The subzone is well established in southern England, on the Dorset coast (Lang, 1926) and in the Stowell Park Borehole (Spath, 1956 : 150). To the north of the Massif Central (Mouterde, 1953 : 404) stratigraphical evidence is inadequate. In northern Germany *A. obtusum* and *A. stellare* have been recorded from the same bed (Hoffmann, 1950*a* : 82) but as the bed is 15–16 metres thick they may be in sequence ; *A. obtusum* alone is recorded from a lower horizon.

Promicroceras planicosta (J. Sowerby) and *Xipheroceras dudressieri* (d'Orbigny) occur in the subzone but both range up into the succeeding Stellare Subzone (Spath, 1956 : 150).

Stellare Subzone

(Pl. 67, fig. 2)

Index species. *Asteroceras stellare* (J. Sowerby, 1815 : 211, pl. 93). The lectotype, designated by Donovan (1954 : 32), was refigured by Wright (1880, pl. 22, figs. 3–5).

Nomenclature. Dumortier (1867 : 95) recognized " Couches à *Ammonites stellaris* " as a subdivision of his Oxynotus Zone (see p. 456) ; they were probably equivalent to Oppel's Obtusum Zone. In a restricted sense, a Stellare Zone was placed between Obtusum and Oxynotum by Buckman (1910*a* : xvi), and a Stellare Subzone of the Obtusum Zone was accepted by Lang (1914 : 320). The Landrioti Zone (Lang, 1926 : 159) is a synonym.

Stratigraphy. A zone or subzone characterized by *Asteroceras stellare* has long been recognized by English authors as marking a distinct horizon above that of *A. obtusum*, but continental stratigraphers have not generally accepted it, although the index species is widely distributed in France and Germany according to records in the literature.

Denotatus Subzone

(Pl. 66, fig. 4)

Index species. *Eparietites denotatus* (Simpson, 1855 : 76). The holotype was figured by Buckman (1912, pls. 67A, B).

Nomenclature. The term was first used by Buckman (1919 : 120*b*) as " *stellare* (*denotatus*) zone " in the explanation of a plate. Earlier Buckman (1918 : 271) had placed the hemera of *denotatus* above that of *stellare*. Spath recognized a separate " *denotatus* zone " in 1925 (p. 264) and in 1942 placed the Denotatus Subzone at the top of the Obtusum Zone. The Lacunatum Zone of Söll (1956 : 375) is a synonym (see below).

Stratigraphy. In Britain the subzone is well developed in Yorkshire, where, however, the presence of the other subzones of the Obtusum Zone is said to be doubtful (Spath, 1925 : 264). *Eparietites* occurs in the Vale of Gloucester and the subzone is probably present in the Stowell Park Borehole (Spath, 1956 : 150) and in Somerset, but on the south coast it is represented by a non-sequence (Lang, 1926 : 158).

In Württemberg the subzone has recently been recorded under the name of Lacunatum Zone, from which *Eparietites impendens* (Young & Bird) is noted (Söll, 1956 : 375, 382). According to Frebold (1925 : 15, 16) the corresponding strata are absent from north-western Germany. There is no evidence for the presence of the subzone in France.

The genus *Eparietites* is probably confined to the subzone, and *Aegasteroceras* persists into it from earlier beds.

OXYNOTUM ZONE

(Pl. 66, fig. 5 ; Pl. 67, fig. 3)

Index species. *Oxynoticeras oxynotum* (Quenstedt, 1843 : 161 ; figured 1845, pl. 5, figs. 11*a*, *b*).

Nomenclature. The zone was introduced by Oppel (1856 : 54). Dumortier (1867 : 93–97) extended the zone to include the Turneri to Raricostatum Zones (of the present paper) inclusive " Pour ne pas trop multiplier les subdivisions ", but recognized four subdivisions within it. The Bifer Zone of Emerson (1870 : 278, 280, 290) included rather more than Oppel's Oxynotum Zone and is rejected. Buckman's *polyophyllum*, *oxynotum*, *biferum*, *simpsoni*, *Gagaticeras*, *lacunata*, and *subpolita* hemerae (1930 : 45) are included in the zone.

Stratigraphy. The subdivision here adopted is into two subzones, Spath's Lymense Subzone at the top being rejected for general use. *Oxynoticeras lymense* (Wright) is found only in Dorset, and the correlation of the beds in which it occurs is uncertain (Spath, 1956 : 149). The Lymense beds of Dorset are transferred to the Densinodulum Subzone of the Raricostatum Zone (see p. 459).

The Schlotheimiid genus *Angulaticeras* is present throughout the zone, but is of sporadic occurrence.

Simpsoni Subzone

(Pl. 67, fig. 4)

Index species. *Oxynoticeras simpsoni* (Simpson, 1843 : 37–38). The holotype was figured by Buckman (1912, pls. 66a, b).

Nomenclature. First used as a subzonal index by Spath (1942) : a *simpsoni* hemera had been introduced by Buckman (1918 : 269), and a *simpsoni* zone (?)[1] placed between *lacunatum* and *bifer* by Spath (1925 : 264). The Gagateum Zone of Hoffmann (1944 : 289) and the Praecursor Zone of Söll (1956 : 376) are synonyms.

Stratigraphy. The subzone is present in Yorkshire and Lincolnshire, but on the Dorset coast, and probably elsewhere in the south of England, it is missing owing to a non-sequence. It has been recognized in North Germany (Hoffmann, 1944 : 289, as Gagateum Zone). In Württemberg, Söll has recently set up a Praecursor Zone which occupies the stratigraphical position of the Simpsoni Subzone and is here correlated with it. The index species, *Oxynoticeras praecursor* Söll, known only from septate inner whorls, appears not very different from *O. simpsoni*. The presence of the Simpsoni Subzone in the Côte d'Or may be indicated by the record of *Gagaticeras gagateum* (Young & Bird) by Mouterde (1953 : 278, 280, 287).

In addition to the index species, *Gagaticeras gagateum* occurs in the subzone, but may also range higher. *Cheltonia* is present and it also occurs in the Oxynotum Subzone. *Slatterites* belongs to this subzone, to judge from its association with *O.* aff. *simpsoni* noted by Spath (1925 : 110, expl. of fig. (*c*)), and from French records (Mouterde, 1953).

Oxynotum Subzone

(Pl. 66, fig. 5 ; Pl. 67, fig. 3)

Index species. As for Oxynotum Zone.

Nomenclature. The index species was used in a restricted stratigraphical sense by Buckman (1918 : 269) who introduced an *oxynotum* hemera.

Spath (1942) adopted the term Bifer Subzone for this subdivision, with Oxynotum (*s.s.*) as an alternative.

It is doubtful whether Spath intended to restrict the broad Bifer Zone of Emerson (1870 : 278, etc.) ; more probably he derived his subzone from the *biferum* hemera of Buckman (1918 : 269). *Oxynoticeras oxynotum* is now used as the subzonal index on account of uncertainty as to the vertical range of *Bifericeras bifer* (Quenstedt) (see below).

Stratigraphy. The subzone corresponds to the range of the index species. *Cheltonia* occurs throughout the subzone but is not restricted to it. In Württemberg, *Bifericeras bifer* is restricted to the lower part of the subzone and Söll (1956 : 371, 377) has therefore recognized a Bifer Subzone at the base of his Oxynotum Zone (= Oxynotum Subzone of this paper). In some British sections *B. bifer* and related species are commonest in the upper part of the subzone, and Söll's arrangement is not, therefore, of general application. Species of *Bifericeras* allied to, if not identical with *B. bifer* occur also in the succeeding Densinodulum Subzone. *Angulaticeras* may be found at any level in the subzone, and *Palaeoechioceras*[1] occurs in southern England.

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[1] The status of the subdivisions in Spath's 1925 Table is not clear. Some of them are referred to in the text as zones.

The subzone is present in England, but is absent from the Dorset coast. It is generally absent from North-west Germany (Hoffmann, 1949 : 114), but the fauna is well known from Swabia. Mouterde (1953 : 119, 349) records the subzone from the Côte d'Or and the northern side of the Massif Central, in condensed facies.

RARICOSTATUM ZONE

(Pl. 68, fig. 1)

Index species. *Echioceras raricostatum* Zieten (1831 : 18, pl. 13, figs. 4*a–c*). The type figure is poor but the species is believed to be represented by Quenstedt (1845, pl. 4, figs. 3*a–d*). See Donovan (1958*a* : 18).

Nomenclature. The zone was introduced by Oppel (1856 : 56). It includes the following of Buckman's hemerae (1930 : 43–45) : *Radstockiceras, rothpletzi* [1st *Echioceras*], *glevense*, armatoid, *lymense, densinodulum* [*densinodum*], *subplanicosta, bispinigerum, anguiforme, miles, simile, costidomus, rhodanicum, tubellus, boreale, raricostatoides, Plesechioceras, planum, macdonnellii, aplanatum* [*Metechioceras*], *Euechioceras* and *defluxum* : possibly a record number for a single zone. There is very little significance in the order in which these hemerae were placed by Buckman : many of them represent hypothetical horizons and cannot be placed in their respective subzones.

Stratigraphy. The zone as now interpreted is larger than the Raricostatum Zone of Spath (1942) by the inclusion at the base of the beds attributed to his Lymense Zone (see above, p. 456). The upper three subzones are those accepted by Spath, but the lowest is replaced by the Densinodulum Subzone, as explained below.

The zone corresponds to the range of the genus *Paltechioceras*. In some areas this genus is found only above the Raricostatum Subzone, but evidence from Raasay and from unpublished sections in southern England shows that it occurs also in the Densinodulum Subzone. The Eoderoceratidae *Bifericeras*, *Crucilobiceras* and " *Hemimicroceras* "[2] occur in the earlier part of the zone, and *Eoderoceras* probably persists throughout.

Spath (1956 : 148) thought that a Tubellus Subzone might eventually be established at the top of the Raricostatum Zone or at the base of the Jamesoni Zone. Recent evidence shows that " *Tubellites* " *tubellus* (Simpson), probably a species of *Gemmellaroceras*, is either long ranging, or likely to be confused with similar small, smooth species or smooth inner whorls of larger species, at widely different horizons. It has therefore no stratigraphical value.

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[1] *Hypechioceras* Spath (1956 : 149) is a synonym.

[2] i.e. the species described under this name by Trueman & Williams (1927), which require a new generic name since *Hemimicroceras*, as properly defined, appears to be synonymous with *Bifericeras*.

Densinodulum Subzone

(Pl. 67, fig. 5)

Index species. *Crucilobiceras densinodulum* Buckman (1923*a*, pl. 442).

Nomenclature. The Densinodulum Zone was introduced by Lang (1926 : 157) in a more restricted sense than now used ; the index species had already been used for a hemera by Buckman (1923*a*, pl. 442). Several other zones introduced by Lang (1926) have equal priority : their indices are *Eoderoceras bispinigerum* (Buckman), *E. obesum* (Spath), and *Crucilobiceras ornatilobatum* (Spath). Bispinigerum Subzone was preferred by Spath (1942) ; for discussion see below. The Lymense Zone (Spath, 1925 : 263 ; Lang, 1926 : 157) and Subplanicosta Zone (Hoffmann, 1948 : 154) are also synonyms.

The name Armatum Subzone, if considered to have priority, should be applied to this subzone, but was rejected by Spath (1942) and the present authors are in agreement. It dates from Oppel (1856 : 117, etc.) who used it for basal beds of the continental Middle Lias (i.e. the Pliensbachian Stage) but pointed out that this usage was conditional on his having correctly identified Sowerby's *Ammonites armatus* in Swabia. His identification has proved to be incorrect (the ammonites in question are *Apoderoceras*). Oppel's Armatum Zone was therefore misnamed and the true *Ammonites armatus* is not accepted as having priority as a zonal index from 1856.

Stratigraphy. The subzone replaces the Lymense and Bispinigerum Subzones of Spath (1942) for, except locally, it is not possible to distinguish more than one subzone between the Oxynotum and Raricostatum Subzones. The index species ranges through the " Lymense " and " Bispinigerum " Subzones in Dorset, and is a common ammonite in a number of areas. It is therefore preferred to the index species of equal priority, mentioned above, which range through only part of the subzone, and which are less abundant as fossils.

The base of the subzone in most sections is defined by the first appearance of *Crucilobiceras*. Rarely, a *Paltechioceras* fauna is found at this level, and where present may be taken to mark the base of the subzone and of the Raricostatum Zone (see above). The top of the subzone is marked by the incoming of *Echioceras*. *Crucilobiceras densinodulum* ranges above this level, for example on the Dorset coast, but it does not appear possible to find a more suitable index species. " *Hemimicroceras* " is characteristic of the subzone in some places (for instances the Stowell Park Borehole, Spath, 1956 : 148–149) although it has not been found on the Dorset coast, but " *H.*" *subplanicosta* (Oppel) ranges up into the Raricostatum Subzone at Stowell Park and in North-west Germany (Hoffmann, 1950 : 110). This species was used as a zonal index for the present subzone by Hoffmann (1948 : 154, see also 1944 : 289) but is no more suitable than *C. densinodulum* which has priority.

Species of *Eoderoceras*, including *E. bispinigerum* (Buckman) and *E. armatum* (J. Sowerby), occur in the subzone in Dorset, but species close to the last are found at higher horizons. *Gleviceras* similarly occurs throughout the subzone and also ranges higher ; the succession of species is not known.

Raricostatum Subzone

(Pl. 68, fig. 1)

Index species. See Raricostatum Zone.

Nomenclature. See Raricostatum Zone. *Echioceras raricostatoides* Vadasz was used as the index of a hemera by Buckman (1918, Table facing p. 267) and of a zone by Lang (1926 : 155). Spath (1942) adopted it in preference to Raricostatum (*s.s.*), but in the present writer's view (Donovan, 1958*a* : 19) the available evidence does not allow a decision as to whether *E. raricostatoides* is a separate species from *E. raricostatum.* Exhaeredatum Zone of Lang (1926 : 155) is a synonym, as explained below. Aeneum Zone of Lang (1926 : 155) is also a synonym (Spath, 1956 : 148).

Stratigraphy. The base of the subzone is marked by the first appearance of *Echioceras,* and the top by its replacement by *Paltechioceras. Echioceras raricostatum* is usually common, whilst *E. aeneum* Trueman & Williams occurs in the lower part of the subzone and may locally appear below *E. raricostatum,* as on the Dorset coast (Lang, 1926 : 155). The genera *Bifericeras* and *Crucilobiceras* occur in the subzone, and *Bifericeras* probably does not range higher ; it is represented by the smooth *B. parvum* (Buckman). A bed in Dorset with the rare genus *Epideroceras* was separated as Exhaeredatum Subzone (see above), but later collecting showed it to belong to the Raricostatum Subzone (Spath, 1956 : 148).

The subzone has been widely recognized throughout the province by the presence of the index species.

Macdonnelli Subzone

(Pl. 67, fig. 6)

Index species. *Leptechioceras macdonnelli* (Portlock, 1843 : 134, pl. 29A, fig. 12). The holotype was refigured by Wright (1880, pl. 37, figs. 3, 4).

Nomenclature. First used as the " Zone of *Leptechioceras macdonnelli* " by Lang (1926 : 155), deriving probably from a hemera of the same name (Buckman, 1918, Table V). Spath (1942) reduced it to a subzone of the Raricostatum Zone.

Stratigraphy. The subzone is defined by the range of the genus *Leptechioceras,* which in Britain lies above that of *Echioceras.* In thick facies there is a gap between the ranges of the two genera, while in thinner developments they may be associated, possibly due to condensation of the sequence. *Paltechioceras* exists throughout the subzone (see remarks above on its range, p. 458). Eoderoceratidae occur but are generally less common than Echioceratidae.

The subzone is present in Raasay (Hebrides), Yorkshire and the Stowell Park Borehole, and typical species are recorded from condensed sequence in the Radstock area of Somerset (Tutcher & Trueman, 1925 : 645). On the Dorset coast it falls in the non-sequence between beds 104 and 105 (Lang, 1928 : 195). On the Continent, it has not been identified in actual sections, but *Leptechioceras* occurs in the Côte d'Or as *L. nodotianum* (d'Orbigny).

In North Germany Echioceratidae appear to be rare in the later Raricostatum

Zone and Hoffmann has used zones based on Eoderoceratidae. In 1944 (pp. 289–290) the zone of *Eoderoceras postarmatum* Hoffmann was placed above the Raricostatoides Zone (i.e. Raricostatum Subzone of the present paper), but in 1948 (p. 159) it was replaced by the zone of *E. miles* (Simpson), on the grounds that this species is more common in North-west Germany than *E. postarmatum* (Hoffmann, 1950 : 78). The Miles Subzone will presumably continue to be used in North-west Germany, to replace Macdonnelli and Aplanatum Subzones of the present scheme, but where Echioceratidae are present they are superior for stratigraphical purposes, because species of *Eoderoceras* are not very easy to identify and are comparatively long ranging.

According to Hoffmann (1950 : 77), the Miles Subzone is absent from South-west Germany.

Aplanatum Subzone

(Pl. 68, fig. 2)

INDEX SPECIES. *Paltechioceras aplanatum* (Hyatt, 1889 : 146, figs. 21, 24). A photograph of the holotype was published by Buckman (1926, pl. 640).

NOMENCLATURE. First used, as a zone, by Lang (1926 : 155) ; introduced as a hemera by Buckman (1918, Table V). In 1942 Spath placed it as the uppermost subzone of the Raricostatum Zone of Oppel.

STRATIGRAPHY. The index species is believed to be restricted to the subzone, but other species of *Paltechioceras* occur at horizons from the base of the Raricostatum Zone upwards (see above, p. 458). Where the Macdonnelli Subzone can be recognized, the Aplanatum Subzone may be conveniently defined as the part of the Raricostatum Zone lying above it.

The known distribution of the subzone is similar to that outlined for the Macdonnelli Subzone ; though well established in Britain, there is little evidence from the Continent. In North-west Germany the beds attributed to the subzone in Britain are presumably represented by part of the Miles Subzone which is discussed above. In France, on the northern border of the Massif Central, Mouterde (1953 : 404) notes "*Plesechioceras nodotianum*" (*recte Leptechioceras*) and "*Euechioceras*" (*recte Paltechioceras*) as occurring above *Echioceras raricostatum*.

PLIENSBACHIAN STAGE

The term Charmouthian, usually attributed to Mayer-Eymar (1864) but probably first published by Renevier (1874 : 242, pl. 6) is synonymous with Oppel's Pliensbachian and with d'Orbigny's long-rejected Liasien. Renevier himself did not favour the term, but it has been used by various authors. Rollier (1915) proposed to restrict the meaning of Charmouthian to Margaritatus and Spinatum Zones, but he had already been forestalled in the usage : Buckman (1910*a* : xvi) had unjustifiably used the term in a different way, namely for the zones from Raricostatum to Davoei inclusive. Lang (1912) maintained that, if used at all, Charmouthian should be understood in its original sense.

LOWER PLIENSBACHIAN OR CARIXIAN SUBSTAGE

The natural division of the stage into two parts at the appearance of the Amaltheidae was recognized by Oppel (1856 : 116). Carixian was proposed by Lang (1913) as an alternative to Lower Pliensbachian. Buckman subdivided the Carixian of the present paper (part of his Charmouthian ; see above) into Wessexian and Hwiccian Stages[1] (1917 ; 1918 : 263, 266), the division between the two falling within the Ibex Zone. These names were introduced to fit Buckman's hemeral system and are now considered superfluous, especially because they cut across the long-accepted zonal boundaries.

As originally defined Buckman's Deroceratan Age corresponded to the Pliensbachian Stage plus the Raricostatum Zone. It was later much restricted, and in Buckman's final scheme Deroceratan (*pars*), Polymorphitan and Liparoceratan Ages fall in the Lower Pliensbachian.

Oppel's zones are used here. The Jamesoni Zone is slightly restricted, by the transference of Masseanum Subzone from the top of the Jamesoni Zone to the base of the Ibex Zone, resulting in a more balanced arrangement. Four subzones are now recognized in the Jamesoni Zone as thus restricted. The Davoei Zone remains as used by Spath (1942) with the substitution of Capricornus for Lataecosta as the middle subzone.

JAMESONI ZONE

(Pl. 68, fig. 3)

INDEX SPECIES. *Uptonia jamesoni* (J. de C. Sowerby, 1827 : 105, pl. 555, fig. 1).

NOMENCLATURE. The zone was introduced by Oppel (1856 : 118).

STRATIGRAPHY. The extent of the zone in terms of modern detailed stratigraphy is adequately indicated by Oppel's list of characteristic ammonites, bearing in mind that his *Ammonites armatus* was misidentified (see p. 459). According to his definition it includes beds from the Taylori Subzone to the Masseanum Subzone inclusive. The Masseanum Subzone is here excluded, for reasons discussed below (see Ibex Zone).

Taylori Subzone

(Pl. 68, fig. 5)

INDEX SPECIES. *Phricodoceras taylori* (J. de C. Sowerby, 1826 : 23, pl. 514, fig. 1).

NOMENCLATURE. The subzone or horizon of *P. taylori* was introduced by Spath (1923*a* : 9). Synonyms are : Leckenbyi Zone (Lang, 1928 : 195) ; Nodogigas-Taylori Zone (Hoffmann, 1948 : 159) ; Peregrinum Subzone (Spath, 1923*a* : 9). The Armatum Zone as incorrectly used by Oppel and many other authors (see p. 459) is a synonym.

Buckman's hemerae (1930 : 43, 44) of *armatum*, *leckenbyi*, *Phricodoceras*, *peregrinus* and *phyllinus* probably all fall within the subzone.

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[1] Called ages by Buckman, but properly stages since they were founded on geographical names. Ages were based on fossil names, but Buckman sometimes confused the two terms ; see Arkell (1933 : 23–25).

Stratigraphy. The subzone includes the beds separated as the Peregrinum Zone in Dorset, and *P. taylori* is used as the index, following Spath (1942), in preference to *Gemmellaroceras peregrinum* (Haug) which has equal priority, because it is more distinctive. The subzone is also characterized by the genus *Apoderoceras*, and is recognized throughout the province.

Polymorphus Subzone

(Pl. 68, fig. 4)

Index species. *Polymorphites polymorphus* (Quenstedt, 1845 : 86, pl. 4, figs. 9–13).

Nomenclature. Introduced by Spath (1923*a* : 9). The " *caprarius* (= lower *polymorphus*) " zone of Dorset, mentioned by Spath (1926 : 47, note 1) is a synonym. Includes the *caprarius*, *polymorphus* and *trivialis* hemerae of Buckman (1918 : 266 ; 1925 : 77 ; 1930 : 43).

Stratigraphy. The subzone was abandoned by Spath (1942), but there is an interval, in the British successions, between the Taylori and Brevispina Subzones for which it is convenient to have a name. Sufficiently detailed stratigraphy from continental localities is not available. In North-west Germany this part of the sequence seems to be absent or condensed, to judge from borehole sections (Hoffmann, 1950 : 100–119), and the sections on the north side of the Massif Central (Mouterde, 1953) have the same disadvantage. *Radstockiceras* (= *Metoxynoticeras*) occurs in the subzone, and *Platypleuroceras caprarium* (Quenstedt) characterizes the upper part.

Brevispina Subzone

(Pl. 69, fig. 1)

Index species. *Platypleuroceras brevispina* (J. de C. Sowerby, 1827 : 106, pl. 556, fig. 1). Sowerby's figured specimen was refigured by Wright (1880, pl. 32, figs. 2, 3).

Nomenclature. The Brevispina Zone dates from von Seebach (1864 : 21) who used it in a very wide sense. A subzone of *P. brevispina* was used by Spath (1922*a* : 550 ; 1923*a* : 9). The subzone includes the *brevispina* and *Platypleuroceras* hemerae (Buckman, 1918 : 266 ; 1930 : 43).

Stratigraphy. The subzone has been widely recognized by the presence of the index species, although Hoffmann (1950 : 77) does not separate it from his Jamesoni Zone. It includes the last species of *Polymorphites*, such as *P. trivialis* (Simpson) and *P.* cf. *quadratus* (Quenstedt).

Jamesoni Subzone

(Pl. 68, fig. 3)

Index species. As for the zone.

Nomenclature. None of the alternatives to the use of *Uptonia jamesoni* as a subzonal as well as a zonal index is entirely satisfactory. They are : Obsoleta Zone (Lang, 1928 : 193), Bronni Subzone (Spath, 1942 : 265) and Pettos Zone (Thompson, 1899 : 75). The *bronni*, *obsoleta*, *jamesoni* and *pettos* hemerae fall within the subzone (Buckman, 1918 : 266 ; 1930 : 42–43).

Stratigraphy. The subzone is defined by the range of the index species. Spath (1922*a* : 550 ; 1923*a* : 9) and Lang (1928 : 192–193) placed the horizon of *Uptonia obsoleta* (Simpson) below that of *U. jamesoni*. *U. obsoleta* may in some areas be found in association with *Platypleuroceras brevispina*. *Uptonia bronni* (Römer) is restricted to the upper part of the subzone. The Pettos Zone was set up for a horizon below that of *U. jamesoni* in Warwickshire, England, but on the Dorset coast *Coeloceras pettos* (Quenstedt) occurs at the top of the subzone. *C. pettos* is too rare to be suitable as an index fossil.

The subzone is recognized in Britain and on the north side of the Massif Central (Mouterde, 1953 : 153, 200).

IBEX ZONE

(Pl. 69, fig. 4)

Index species. *Tragophylloceras ibex* (Quenstedt, 1843 : 179, and 1845, pl. 6, fig. 6).

Nomenclature. The zone was first used by Oppel (1856 : 122).

Stratigraphy. *Tragophylloceras ibex* occurs in the lower part of the zone in Dorset, being replaced in the Luridum Subzone by *T. loscombi* (J. Sowerby), which ranges up into the Davoei Zone. The zone is now used in a wider sense than that of Oppel, by the inclusion of the Masseanum Subzone at the base. Oppel recorded *Ammonites masseanus* d'Orbigny as a fossil of the Jamesoni Zone and cited it from the same horizon as *Ammonites jamesoni* (1856 : 123), but in areas where detailed collecting has been carried out neither *Uptonia jamesoni* nor any other species of *Uptonia* persists into the beds with *Tropidoceras masseanum*, so it is more convenient to terminate the Jamesoni Zone with the extinction of *Uptonia*, and take the Masseanum Subzone (as did Mouterde, 1953 : 408) as the base of the Ibex Zone.

Masseanum Subzone

(Pl. 69, fig. 2)

Index species. *Tropidoceras masseanum* (d'Orbigny, 1844 : 225, pl. 58). The holotype was refigured by Nicklès (1903, pl. 8).

Nomenclature. Introduced by Spath (1923*a* : 9) as the uppermost subdivision of Oppel's Jamesoni Zone. Includes the *masseanus* and *ellipticum* hemerae of Buckman (1918 : 266 ; 1930 : 42).

Stratigraphy. The base of the subzone is marked by the appearance of the genus *Tropidoceras*, the index species being accompanied by allied species including *T. ellipticum* (J. Sowerby) and *T. galatense* (Gemmellaro). The subzone is recognizable throughout Britain, and on the north side of the Massif Central (Mouterde, 1953 : 297, 408). *Tropidoceras* cf. *masseanum* is recorded from North Bavaria (Krumbeck, 1936 : 194, 199, etc.), from condensed facies in which the stratigraphical order of the ammonites has not been determined.

Valdani Subzone

(Pl. 69, fig. 5)

Index species. *Acanthopleuroceras valdani* (d'Orbigny, 1844 : 255, pl. 71).

Nomenclature. Introduced as the Zone of *Ammonites Valdani* by Collenot (1869 : 166), it was in 1942 reduced to the status of a subzone of the Ibex Zone by Spath. The Actaeon, Maugenesti and Centaurus Subzones (Spath, 1923*a* : 9) are synonyms (see below). The last-named was perhaps derived from Buckman's *centaurus* hemera, or from the Centaurus Zone which Emerson (1870 : 278, 280, 302) established as a subdivision of von Seebach's Brevispina Zone. The Venarensis Zone (Collenot, 1869 : 166), which Collenot placed above his Valdani Zone, has equal priority and is a synonym. It is unsuitable because *Ammonites venarensis* Oppel is not well known and appears to be rare.

The subzone includes the *ibex, maugenesti, valdani, actaeon, cheltiense, carinatum* and *centaurus* hemerae of Buckman (1918 : 264 ; 1925 : 77 ; 1930 : 42).

Stratigraphy. Spath (1923*a*) divided the beds now included in the subzone into the Maugenesti, Actaeon and Centaurus Subzones. It now appears that in some areas the order of the index species *Acanthopleuroceras maugenesti* (d'Orbigny) and *Tropidoceras actaeon* (d'Orbigny) is reversed, for example on the borders of the Massif Central (Mouterde, 1953 : 153), and Spath (1942) himself later adopted the prior Valdani Subzone to include both these horizons. He retained the Centaurus Subzone above Valdani, but recent evidence from England shows that the range of *Beaniceras*[1] *centaurus* (d'Orbigny) overlaps that of *Acanthopleuroceras valdani* and *A. maugenesti*. Association of the two genera is also recorded from the north side of the Massif Central (Mouterde, 1953 : 408) where it may, however, be due to condensation of the sequence.

The subzone is widely recognized throughout the province. *Acanthopleuroceras* is characteristic of the subzone, and in some areas appears to be accompanied by species of *Tropidoceras* such as *T. actaeon, T. calliplocoides* (Spath) and *T. stahli* (Oppel), although on the Dorset coast the latter fauna succeeds *A. valdani. Tropidoceras* in any case persists into the next subzone (see below). *Beaniceras centaurus*, in some areas at least, survives into higher beds than *Acanthopleuroceras valdani*, but these beds are included in the Valdani Subzone, of which the upper limit is taken at the first appearance of *Beaniceras luridum.*

Luridum Subzone

(Pl. 69, fig. 6)

Index species. *Beaniceras luridum* (Simpson, 1855 : 46). The type of the species was figured by Buckman (1913, pl. 73).

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[1] The author of this section prefers to regard *Beaniceras, Androgynoceras* s.s. and *Oistoceras* as subgenera, marking successive stages in the evolution of the genus *Androgynoceras* (Donovan, 1954 : 16). They are here written as genera for the sake of brevity.

Nomenclature. The subzone is here proposed for the first time.

Stratigraphy. The new subzone is proposed for the uppermost part of the Ibex Zone, in which *B. centaurus* is replaced by *B. luridum* and allied " species " such as *B. geyeri* (Spath) and *B. subluridum* Spath. The index species accompanied by *Liparoceras* species such as *L. elegans* Spath, *L. pseudostriatum* Trueman and *Tragophylloceras loscombi* (J. Sowerby), is present in Dorset in the Belemnite Stone (Lang, 1928 : 189, bed 121), but this part of the Dorset coast sequence is condensed and incomplete. The subzone is distinct in the thicker clay facies in Gloucestershire, and is well shown in the brick pit near Blockley station, mentioned by Richardson (1929 : 15). The ammonite succession here has been worked out by Dr. J. H. Callomon, who is preparing an account for publication. The type of *B. luridum* comes from the Yorkshire coast, but its exact horizon is apparently unknown. On the northern side of the Massif Central, the index species is recorded by Mouterde (1953 : 408) as characteristic of a horizon at the top of the Ibex Zone, accompanied by *Liparoceras kilsbiense*, above the beds with *Acanthopleuroceras* and *B. centaurus*.[1] The subzone has not been definitely identified in Germany.

DAVOEI ZONE

(Pl. 70, fig. 1)

Index species. *Prodactylioceras davoei* (J. Sowerby, 1822 : 71, pl. 350).

Nomenclature. The zone was introduced by Oppel (1856 : 126). The Capricornus Zone, when set up, was a synonym, but is now retained as a subzone. The Fimbriatus Zone of von Schloenbach (1863) presumably includes the Davoei Zone.

Buckman's Liparoceratan Age corresponds to the Davoei Zone, which includes the hemerae of " *henleyi* ", *lataecosta*, *davoei*, *daedalicosta* and *Oistoceras* [*striatum*], but little significance can be attached to the order in which they were listed by Buckman (1918 : 264 ; 1930 : 42).

Stratigraphy. The zone was subdivided by Lang (1914, Table facing p. 308 ; 1936 : 431–435), but the Bechei Subzone introduced in 1936 has since been abandoned (see Capricornus Subzone, below) and a three-fold subdivision, founded on species of the family Liparoceratidae, remains. *Prodactylioceras davoei* occurs in the Capricornum and Figulinum Subzones. In addition to Liparoceratidae and *Lytoceras*, *Tragophylloceras loscombi* occurs throughout the zone.

Maculatum Subzone

(Pl. 70, fig. 4)

Index species. *Androgynoceras maculatum* (Young & Bird, 1822 : 248, 327, pl. 14, fig. 12). The holotype was figured by Buckman (1912, pl. 45A, B). For full description and illustration see Spath (1938 : 126).

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[1] Mouterde states that *B. centaurus* occurs in England at the level at which he finds *B. luridum* ; this is evidently a misconception.

NOMENCLATURE. The term was first used, as a zone, by Lang (1936 : 434). Spath (1938 : 34 ; 1942) employed it as the lowest subzone of Oppel's Davoei Zone. The Striatum Zone of Buckman (1910*a* : xvi), which originated as the hemera of *Liparoceras striatum* (Buckman, 1898, Table facing p. 450), is a synonym, but is considered invalid as the index species when proposed (as *Nautilus striatus* Reinecke, 1818) was a homonym of *Nautilus striatus* J. Sowerby, 1817. It is, in any case, uncertain whether Buckman correctly identified Reinecke's *striatus* and correctly placed it stratigraphically.

STRATIGRAPHY. The subzone corresponds to the range of *Androgynoceras maculatum*, and is recorded on the Dorset coast (Lang, 1936), in the Stowell Park Borehole (Spath, 1956 : 145) and in Yorkshire (Spath, 1938 : 26–27). It has not been separated from the Capricornus Subzone in Germany, although the index species has been recorded from Württemberg (Spath, 1938 : 132–133). In France, on the borders of the Massif Central, the index species is recorded from the same bed as *A. lataecosta* (J. de C. Sowerby), a species of the Capricornus Subzone (Mouterde, 1953 : 152, 322) ; this may well be due to condensation of the sequence. In spite of the present lack of confirmation from the Continent, the subzone is retained as its consistent position in England suggests that it marks an evolutionary stage in the *Androgynoceras* lineage, and may be of use over a wide area.

Capricornus Subzone

(Pl. 69, fig. 3)

INDEX SPECIES. *Androgynoceras capricornus* (Schlotheim, 1820 : 71). Lectotype figured by Spath (1938 : 150, pl. 23, fig. 1).

NOMENCLATURE. The Capricornus Zone was first used by Wright (1863 : 79) who stated that the Davoei Zone of Oppel (which has priority) was a synonym. No reason for the substitution was given. The term is retained in a more restricted sense as a subdivision of the Davoei Zone. The Bechei Zone (Lang, 1936 : 432) is now included in the Capricornus Subzone, its general applicability being unconfirmed (Spath, 1956 : 145). The following are also junior synonyms : Daedalicosta Zone (Trueman, 1919 : 252), of which the index species is said to be a synonym of *Liparoceras* (*Becheiceras*) *bechei* (J. Sowerby) (Spath, 1938 : 75) ; Henleyi Zone (Collenot, 1869 : 166) ; Lataecosta Subzone (Lang, 1914, Table facing p. 308) as restricted by Lang (1936 : 433) ; *Liparoceras* Subzone (Lang, 1914, Table facing p. 308), superseded by Bechei Zone.

STRATIGRAPHY. The subzone embraces the ranges of *Androgynoceras capricornus* and *A. lataecosta* (J. de C. Sowerby), the latter immediately succeeding *A. maculatum* in Britain. The subzone is widely recognized, although, as remarked in the notes on Maculatum Subzone, it has not been separated from that subzone in Germany or in France. The highest part of the subzone was at one time separated as the Bechei Subzone, which has since been rejected (Spath, 1942 ; 1956 : 145). *Liparoceras* (*Becheiceras*) *bechei* is an indifferent zonal fossil, being difficult to distinguish from later species of the subgenus which range well into the Margaritatus Zone. A horizon of *L.* (*B.*) *bechei* is listed by Krumbeck (1936, Table 28) from northern Bavaria at a higher level (Figulinum Subzone or above), which confirms the unsuitability of the fossil as a subzonal index.

Figulinum Subzone

(Pl. 70, fig. 5)

INDEX SPECIES. *Oistoceras figulinum* (Simpson, 1855 : 47, 48), the type of which was figured by Buckman (1911*a*, pl. 26A). See also Spath (1938 : 162).

NOMENCLATURE. The subzone was introduced by Lang (1936 : 431) as the highest subzone of the Davoei Zone. It superseded the same author's " Subzone of *Oistoceras* " (1914, Table facing p. 308). Hoffmann's zone of *Prodactylioceras davoei* and *Oistoceras curvicorne* is the equivalent of the Figulinum Subzone (Hoffmann, 1949 : 115). Davoei Zone (Oppel, 1856), as strictly interpreted, has priority over Figulinum Subzone, but it is more consistent to subdivide the Davoei Zone by means of species of Liparoceratidae rather than to use Davoei for both zone and subzone.

STRATIGRAPHY. The index species is widely distributed in England, France and Germany. The base of the subzone may be taken at the appearance of *Oistoceras*. *Androgynoceras* s.s. persists into the subzone in some areas, as in Gloucestershire and Lincolnshire (Spath, 1956 : 145), and the borders of the Massif Central (Mouterde, 1953 : 409), *A. capricornus* of the underlying subzone being replaced by *A. artigyrus* (Brown). *Prodactylioceras* appears at about the base of the subzone (just below *Oistoceras* in Dorset, England), and *Liparoceras* (*Becheiceras*) ranges throughout. The subzone is terminated above by the appearance of the *Amaltheus stokesi* fauna, marking the base of the Margaritatus Zone.

UPPER PLIENSBACHIAN OR DOMERIAN SUBSTAGE

The term Domerian was proposed by Bonarelli (1894) for the Margaritatus and Spinatum Zones as defined by Oppel (1856). It is, therefore, an alternative to Upper Pliensbachian, even though the type area of the Domerian is Monte Domero (now known as Monte Domaro), Tuscany, Italy, which is outside the North-west European Province. By definition the Domerian corresponds to the range of the distinctive family Amaltheidae and to the British Middle Lias.

The limits of the Margaritatus and Spinatum Zones are the same as in Oppel's original definitions (1856 : 129ff., 138ff.).

MARGARITATUS ZONE

(Pl. 70, fig. 3)

INDEX SPECIES. *Amaltheus margaritatus* de Montfort (1808 : 91). The neotype was figured by Howarth (1958 : 15, text-fig. 8).

NOMENCLATURE. Introduced by Oppel (1856 : 129). Synonyms are the Algovianum Zone of Buckman (1910*a* : xvi) and the Nitescens Zone of Thompson (1910 :

458); both were based on species of *Arieticeras* which occur widely in the Margaritatus Zone. The "Zone de l'*Ammonites zetes* d'Orbigny" (*Phylloceras*) of Collenot (1869 : 172) is also a synonym. The zone includes the *Seguenziceras* [*algovianum*] and *margaritatus* hemerae of Buckman (1930 : 41–42).

Stratigraphy. The base is clearly defined over most of the area by the sudden appearance of *Amaltheus stokesi*. The range of *Amaltheus* does not distinctly overlap with that of the highest *Oistoceras* at the top of the Davoei Zone, although both have been found in the same bed in Lincolnshire (Howarth, 1958 : xii) and at two localities in North-west Germany (Lange, 1932 : 239; Kumm, 1941 : 283). The top is drawn immediately below the lowest *Pleuroceras*. Spath's divisions (1942) of the zone were founded on Frentzen's monograph (1937) on the Amaltheidae of South-west Germany, but it has been found subsequently that the earliest Amaltheidae fauna is not common in this area and a further subzone of *Amaltheus stokesi* has had to be inserted at the base. All the subzones are recognizable in the Aveyron district of South-east France, but they have not yet been recognized in other areas of France, nor in North Germany.

In the southern part of the province, especially south-eastern France, Hildoceratidae, Dactylioceratidae and Amaltheidae are all common in the Margaritatus and Spinatum Zones. Southwards in the Mediterranean Province Amaltheidae become rare and the other families become abundant, whilst in the central and northern parts of the North-west European Province Dactylioceratidae are absent and Hildoceratidae are far less abundant than Amaltheidae. Zonal schemes founded on the Hildoceratidae in the Mediterranean and on the Amaltheidae in North-west Europe can be correlated against each other in areas such as Aveyron where the two provinces meet.

Stokesi Subzone

(Pl. 70, fig. 2)

Index species. *Amaltheus stokesi* (J. Sowerby, 1818 : 205, pl. 191). The holotype was figured by Howarth (1958, pl. 1, fig. 7).

Nomenclature. First used by Lang (1936 : 431) for the beds at the base of the Margaritatus Zone near Seatown, Dorset. Includes the *fieldingi* and *clevelandicus* hemerae of Buckman (1930 : 42).

Stratigraphy. The subzone corresponds to the range of *Amaltheus stokesi*, for the upper boundary is marked by the appearance of *A. subnodosus* (Young & Bird) and at this level *A. stokesi* is replaced by *A. margaritatus*. There are few other Amaltheidae in this subzone: *Amaltheus bifurcus* Howarth, *A. wertheri* (Lange) and rare examples of *Amauroceras ferrugineum* (Simpson) occur in Britain and *Amaltheus evolutus* Buckman in South-east France. Species of the Hildoceratidae genera *Arieticeras* and *Leptaleoceras* are found in England mainly in this part of the Margaritatus Zone, and there are also representatives of the genera *Tragophylloceras*, *Liparoceras* (*Becheiceras*) and *Metacymbites*.

In most areas of England this subzone is much thicker than any of the other subzones of the Middle Lias and the characteristic ammonites are abundant, but in other areas of the province it is either very thin, yet to be found, or absent. In the Hebrides it is poorly developed and the index ammonite is rare.

The only definite records from France and Germany are at Aveyron, where the " passage beds " and " subzone a_1" of Monestier (1915, 1928) have yielded specimens of *Amaltheus stokesi* and therefore belong to this subzone, and in Swabia where this species and *A. bifurcus* have recently been found. The beds at Aveyron also contain several species of *Protogrammoceras*, *Fuciniceras* and *Arieticeras*.

Subnodosus Subzone

(Pl. 71, fig. 3)

INDEX SPECIES. *Amaltheus subnodosus* (Young & Bird, 1828 : 258, pl. 13, fig. 3). The neotype was figured by Howarth (1958, pl. 2, fig. 11).

NOMENCLATURE. Proposed by Howarth (1955 : 172) in substitution for the Nodifer Subzone of Spath (1942), because *Amaltheus nodifer* Buckman (1911*a* : 25*d*) is a synonym of *A. subnodosus*. The Depressus Zone of Frentzen (1934 : 43) is a senior synonym, for the index species *Ammonites amaltheus depressus* Quenstedt (1885, pl. 39, fig. 19) is pre-occupied. Includes the *boscense* and *acanthoides* hemerae of Buckman (1930 : 42).

STRATIGRAPHY. The subzone corresponds to the range of *Amaltheus subnodosus*. The zone index *Amaltheus margaritatus* first appears at the base of this subzone and soon becomes abundant.

In all British areas this subzone is well developed and fossiliferous ; *Amauroceras* and several species of *Amaltheus* occur but there are few or no representatives of other ammonite families. The subzone can be recognized in several areas of France and Germany. At Aveyron, Monestier's " subzones a_2 and b " (1915, 1928) belong to the Subnodosus Subzone ; Amaltheidae are abundant and include *Amaltheus gloriosus* Hyatt, which is very rare in Britain, and several species of *Protogrammoceras*, *Fuciniceras*, *Arieticeras*, *Prodactylioceras* and *Reynesoceras* are also common. In Swabia, Frentzen's " *nodifer* beds " (1937) belong to this subzone, and a rich fauna of typical Amaltheidae has been described.

Gibbosus Subzone

(Pl. 71, fig. 2)

INDEX SPECIES. *Amaltheus gibbosus* (Schlotheim, 1820 : 66). The lectotype was figured by Howarth (1958 : 18, text-fig. 10).

NOMENCLATURE. As a hemeral index it dates from Buckman (1918 : 262) ; it was used as a zone by Kuhn (1935 : 465) and as a subzone by Spath (1942). Buckman's Laevis Zone (1920 : 68) is a synonym, for in its type area at Raasay, western Scotland, the range of *Ammonites amaltheus laevis* (Quenstedt, *non* Bruguière) (a synonym of *Amauroceras ferrugineum*) is the same as that of *Amaltheus gibbosus*.

STRATIGRAPHY. This subzone corresponds to the range of *Amaltheus gibbosus*.

At the lower boundary the index fossil does not overlap with the range of *A. subnodosus* and at the upper boundary it changes rapidly into the earliest species of *Pleuroceras*. Other common Amaltheidae in this subzone are *Amaltheus margaritatus*, *A.* (*Pseudoamaltheus*) *engelhardti* (d'Orbigny) and *Amauroceras ferrugineum*.

In Britain, Amaltheidae of this subzone are only common in the Hebrides, where they occur at approximately the middle of the Scalpa Sandstone Series (Howarth, 1956). In all English areas the beds are poor in ammonites, but sometimes *A. margaritatus* occurs fairly commonly alone (Howarth, 1955, 1957, 1958 : ix–xii).

In France and Germany, particularly at localities at Aveyron and in Swabia, this subzone is well developed with the characteristic Amaltheidae very common. Monestier's " subzone c " at Aveyron (1915, 1928) belongs to the Gibbosus Subzone, and, although ammonites of families other than Amaltheidae are not so common as in the Subnodosus Subzone, species of *Arieticeras* and *Paltarpites* also occur. In Swabia, Frentzen's " *margaritatus* beds " (1937) belong to this subzone.

SPINATUM ZONE

(Pl. 71, fig. 1)

Index species. *Pleuroceras spinatum* (Bruguière, 1789 : 40). The neotype was figured by Howarth (1958, pl. 7, fig. 2).

Nomenclature. Introduced by Oppel (1856 : 138). The zone includes part of the " Zone de l'*Ammonites acanthus* " of Collenot (1869 : 172) and the *argutus* and *spinatum* hemerae of Buckman (1930 : 41).

Stratigraphy. The Spinatum Zone corresponds to the range of the genus *Pleuroceras*. *Pleuroceras transiens* Frentzen marks the lower boundary and the top is drawn where the Amaltheidae become extinct and are succeeded by an abundant fauna of Dactylioceratidae and Hildoceratidae. In several areas in the Midlands and on the Dorset coast *Dactylioceras directum* (Buckman) had already appeared alongside the last *Pleuroceras* at the top of the Spinatum Zone (Howarth, 1957 : 197–198). Subdivision is made according to the succession of species of *Pleuroceras*. Species of *Amaltheus*, *Pseudoamaltheus* and *Amauroceras* also occur as well as several genera of other families.

In Britain the rocks of this zone show very large differences in facies and thickness from one area to another. In Dorset, Somerset, the Cotswolds and the Midlands the zone consists of the Marlstone Rock Bed of varying thickness and somewhat varying lithology ; in Yorkshire it consists of most of the Ironstone Series, including the main iron-ore producing seams ; in the Hebrides it consists of roughly the upper 100 ft. of the Scalpa Sandstone. In the Aveyron area of France Monestier's " subzone d " (1915, 1928) belongs to the Spinatum Zone. In the Côte d'Or Collenot's Acanthus Zone (1869 : 172) belongs mainly to the Spinatum Zone, for it contains *Pleuroceras spinatum* and other Amaltheidae (Carré, 1876 : 132), but the upper part may belong to the Tenuicostatum Zone if this should prove to be the proper horizon of *Dactylioceras acanthus* (d'Orbigny).

Apyrenum Subzone

(Pl. 71, fig. 5)

Index species. *Pleuroceras apyrenum* (Buckman, 1911*a* : 24*d*). The holotype was figured by Tate & Blake (1876, pl. 8, fig. 2) and Howarth (1958, pl. 6, fig. 1).

Nomenclature. Introduced by Spath (1942) to supersede Frentzen's Bechteri Zone (1934 : 43), for *Amaltheus bechteri* Frentzen (1934 : 40) is a composite species consisting of both *Pleuroceras solare* (Phillips) and *P. salebrosum* (Hyatt) (see Howarth, 1958 : 30, 33). Includes the *lenticulare* and *regulare* hemerae of Buckman (1930 : 41–42).

Stratigraphy. The commonest Amaltheid is *Pleuroceras solare* (Phillips), and the subzone is best defined as corresponding to the range of this species with the lower boundary extended down to include the first appearance of *Pleuroceras transiens* (Fentzen). In the upper half of the subzone *P. spinatum*, *P. apyrenum* and several other species occur. Other genera represented are *Amauroceras* (especially in Yorkshire), *Amaltheus* and *Pseudoamaltheus*.

In Britain this subzone is well developed, though in the Midlands and in the lower half in Yorkshire, ammonites are rare. In the Hebrides and many localities in west and south-west England the *Pleuroceras solare* fauna is abundant, but in Dorset this subzone is highly condensed and absent in places.

In Swabia Frentzen's " *bechteri* beds " (1937) belong to this subzone and contain the characteristic fauna in abundance. At Aveyron the Spinatum Zone is condensed and this subzone has not been separated. In other areas of France and Germany the presence of the subzone is known from numerous specimens of *Pleuroceras solare*.

Hawskerense Subzone

(Pl. 71, fig. 4)

Index species. *Pleuroceras hawskerense* (Young & Bird, 1828 : 258, pl. 14, fig. 6). The type specimen was figured by Buckman (1923, pl. 408).

Nomenclature. As a hemeral index it dates from Buckman (1922 : 453) and it was used as a subzone by Spath (1942). Includes the *paltus* hemera of Buckman (1930 : 41).

Stratigraphy. Comprises approximately the upper half of the Spinatum Zone, the lower boundary being drawn immediately above the highest *Pleuroceras solare*. There are many Amaltheidae, but representatives of other families are rare. In the top half the incoming *Dactylioceras* fauna (especially *D. directum* (Buckman) and allied species) is found in some places.

In Britain the fauna is highly differentiated : in Yorkshire *P. hawskerense* is abundant, together with *Amauroceras ferrugineum* and *Amaltheus reticularis* (Simpson) ; in the Cotswolds, Somerset and Dorset *P. yeovilense* Howarth and large examples of *P. spinatum* are characteristic, and *P. apyrenum* is also present ; in the Hebrides *P. spinatum* occurs alone.

In France and Germany the subzone can be recognized by the presence of *P. spinatum* and *P. hawskerense* above the range of *P. solare*. It comprises Frentzen's "*spinatus* beds" (1937) in Swabia, but it has not been separated at Aveyron. In North-west Germany *Pseudoamaltheus engelhardti* (d'Orbigny) probably ranges up into this subzone, but its limits have not been determined accurately (Kumm, 1941).

TOARCIAN STAGE

The following two zones were included in the Toarcian by Oppel (1856 : 196) :

2. Zone of *Ammonites jurensis*
1. Zone of *Posidonia bronni*

The base of the Bronni Zone was drawn immediately above the highest *Pleuroceras* and below the first appearance of *Dactylioceras* in abundance. The top of the Jurense Zone was drawn between the faunas of *Pleydellia aalensis* below and *Leioceras opalinum*, at the base of the Bajocian, above.

Whitbian and Yeovilian Substages

The names Whitbian and Yeovilian were first introduced as "Ages" by Buckman (1910 : 88) to provide a means of subdividing the Toarcian Stage. They have found some favour since then as substages and their use as such is often convenient, but some redefinition of their limits is necessary. When founding the term Whitbian on the succession in the neighbourhood of Whitby, Yorkshire, Buckman proposed that it should cover the strata which, in the present paper, constitute the Tenuicostatum to Variabilis Zones inclusive, claiming that all these were developed near Whitby. In practice the Variabilis Zone is not known from either Whitby or the neighbouring cliff sections, being cut out by the unconformity at the base of the overlying Dogger (Lower Bajocian). All these localities are situated north-west of the important Peak Fault, and the Variabilis Zone, together with the succeeding Toarcian strata, is fully developed only at Blea Wyke, about six miles south-east of Whitby, where a radically different succession is found on the south-eastern side of the Peak fault. The line separating Whitbian from Yeovilian should, then, be drawn between the Bifrons and Variabilis Zones as interpreted in this paper, forming a convenient demarcation between the disappearance of *Hildoceras*, perhaps the best known of all the Whitby ammonites, and the appearance of the Phymatoceratinae.

The type section of the Yeovilian lacks the precision of the Whitbian succession, being defined merely as "the Somerset–Dorset district", though presumably at or near Yeovil. In its original usage (Buckman, 1910 : 88) the Yeovilian comprised the present Striatulum to Moorei Subzones inclusive, but if the top of the Whitbian is to coincide with the top of the Bifrons Zone then the Yeovilian should commence with the Variabilis Zone. At Barrington the base of the Yeovil Sands (Dispansum Subzone) is underlain by 6 in. of black clays which apparently represent a condensed sequence (Spath *in* Buckman, 1922 : 449). The fauna includes *Hildoceras*, *Haugia*, *Grammoceras*, *Pseudogrammoceras* and *Hammatoceras*, and indicates the presence of horizons ranging from the Bifrons Zone (*pars*) to the Struckmanni Subzone. Therefore the Variabilis Zone is represented in the type area of the Yeovilian.

To follow Buckman rigidly in drawing the upper limit of the Yeovilian between the Moorei and Aalensis Subzones would be to isolate the latter within the upper part of the succession which, by original definition, must necessarily be included in the Toarcian Stage. The separation of the two is also unjustified on palaeontological grounds as they both contain *Dumortieria* in certain European districts. The evidence for the existence of the Aalensis Subzone near Yeovil is well established, and at Haselbury Mills thin blue clays and marls with a typical ammonite fauna are overlain unconformably by Upper Inferior Oolite (Kellaway & Wilson, 1941 : 147). It is noteworthy that Buckman, in his earlier works, did not recognize an Aalensis horizon and placed the " *Moorei*-Beds " of the Cotswolds immediately below the *Opalinum* Beds or Zone, from which he recorded *Grammoceras aalense* (Buckman, 1889 : 463). In addition Buckman (1889 : 451) recorded *Grammoceras aalense* from the " Moorei- and Dumortieria-Beds " in the " Yeovil or Bridport Sands " of Burton Bradstock, and he later (1910 : 89) argued that the top of the Yeovilian ended appropriately with the " finish of the Yeovil Sands ". The borehole at Stowell, about three miles north of Milborne Port, has shown that the topmost 5 ft. of the Yeovil Sands belong to the Aalensis Subzone (Kellaway & Wilson, 1941 : 147–148). Thus the inclusion of the Aalensis Subzone at the top of the Yeovilian is borne out by geological evidence from the type area.

Aalenian " Stage "

Aalenian has frequently been used as a stage or substage to include some part of the Upper Lias. At its original proposal by Mayer-Eymar (1864) the beds included were the " Couches de Boll ou à l'*Amm. torulosus* " at the base, up to the " Couches de Giengen ou à l'*Amm. sowerbyi* " at the top ; it was immediately underlain by the " Couches de Heiningen ou à l'*Amm. jurensis* " at the top of the Toarcian. Later Mayer-Eymar (1881) made it clear that what he meant by the beds with *Amm. torulosus* and *Amm. jurensis* were the Torulosus and Jurense Zones as defined by Oppel (1856). Therefore the base of the Aalenian is drawn between Oppel's Torulosus and Jurensis Zones, i.e. between the Opalinum and Jurense Zones of modern nomenclature, and it coincides with the base of the Bajocian. From the original definitions of these zones, the Aalenian does not, therefore, include the subzone of *Pleydellia aalensis*. Attempts to place the base of the Aalenian at different levels by Renevier, Choffat, Toucas, Buckman and especially Haug's supposed adoption (1892, 1910 : 954) of " l'étage Aalénian dans le sens primitif ", cannot be entertained. Thus the Aalenian cannot be used to include any part of the Lias.

Bronni Zone

Posidonia bronni cannot be used as an index in any scheme of ammonite zones of the Lias, and Oppel himself (1856 : 197) suggested that *Ammonites serpentinus* might be a more satisfactory index. A second alternative index, *Ammonites communis*, was proposed by Wright (1858 : 25), to be superseded later by *Ammonites bifrons*.

The first division of the Bronni Zone was by Reynès (1868 : 63) into a Serpentinus Zone below and a Bifrons Zone above, and finally a third zone of *Ammonites annulatus* was added by Tate & Blake (1876 : 16) below the Serpentinus Zone. This three-fold division of the original Bronni Zone into Bifrons, Serpentinus and Annulatus Zones has proved satisfactory and applicable throughout the province ; subsequent changes in nomenclature alone have now given us the Bifrons, Falcifer and Tenuicostatum Zones, equivalent in every way to the original zones.

Jurense Zone

Oppel's zone of *Pachylytoceras jurense* included ammonites from *Haugia variabilis* at the base up to *Pleydellia aalensis* at the top, and this made the Jurense Zone of roughly the same size as his Bronni Zone. Subdivision of the Jurense Zone has always been made on ammonites other than Lytoceratidae, and a scheme which has since been found to be applicable throughout the province was progressively elaborated by Buckman, mainly on the basis of observations on the Cotswolds Upper Lias, into the seven divisions : *variabilis, striatulum, struckmanni, dispansum, Dumortieria* sp., *moorei* and *aalensis* (Buckman, 1898, Table I, p. 450) (for reasons given below *lilli* is rejected). These were used as subzones of a large Jurense Zone by Spath and Arkell. In Swabia *P. jurense* is common, especially in the middle part of the Jurense Zone, and it ranges up as far as the Aalensis Subzone (Pompeckj, 1896 : 141), but it is much less common elsewhere in Germany and France, and distinctly rare in Britain. Apart from the lack of exact knowledge of the range of *P. jurense*, it would clearly be better to base the zonal and subzonal indices on the same groups of ammonites. At the same time it would be as well to reduce the large size of the Jurense Zone by using several indices in its place. It is now proposed to use three zones with subzones grouped as shown in the Table (p. 441).

Lilli " Subzone "

The *lilli* hemera was introduced by Buckman (1898, Table on p. 450 ; 1898*a* : xii–xiii) as an horizon between *bifrons* below and *variabilis* above. It has been accepted as a valid subzone at the base of the Jurense Zone by Arkell (1933 : 165 ; 1956 : 35) and at the top of the Bifrons Zone by Spath (1942 : 266).

Buckman surmised that by the principle of recapitulation *Haugia* was a descendent of *Lillia*, and therefore *Lillia* must be older (1890 : 145). As *Lillia* is rare in Britain and absent from the Cotswolds he then proposed to recognize the *lilli* horizon in the Cotswolds Sands by its main " contemporary " (i.e. occurring immediately below *Haugia*) ammonite, *Hildoceras semipolitum* Buckman (1898*a* : xiii ; Richardson, 1910 : 115–116). Associates of *H. semipolitum* are species of *Pseudolioceras, Dactylioceras* and *Catacoeloceras* and this is the highest fauna of the Bifrons Zone. Buckman's only record of a true *Lillia* (Buckman & Wilson, 1896 : 687) is from an horizon above the lowest *Haugia*. *Lillia* and *Denckmannia* are now held to be synonyms of *Phymatoceras* and its subgenus *Chartronia*, and Buckman's records of these forms in the lower part of the Cotswolds Sands are all associated with *Haugia* of the Variabilis Zone. The earliest *Haugia* appears before *Phymatoceras*, just the reverse of Buckman's surmise on recapitulation theory.

In Yorkshire, Dean (1954 : 170–171) found that the only *Phymatoceras* recorded, *P. fabale* (Simpson), almost certainly came from the Variabilis Subzone, in association with *Haugia*. The beds containing *Catacoeloceras* that he referred to the Lilli Subzone should be included in the Braunianus Subzone.

In eastern France Mouterde (1953 : 417) found that a Lilli Subzone was not separable, and in Swabia Krumbeck (1944 : 3) was able to show that *Phymatoceras* occurred in the upper half of the Variabilis Zone.

Thus the Lilli Subzone is a synonym of the Variabilis Zone.

LOWER TOARCIAN OR WHITBIAN SUBSTAGE

TENUICOSTATUM ZONE

(Pl. 72, fig. 1)

INDEX SPECIES. *Dactylioceras tenuicostatum* (Young & Bird, 1822 : 247, pl. 12, fig. 8). The neotype was figured by Buckman (1920*a*, pl. 157).

NOMENCLATURE. Introduced by Buckman (1910 : 85) to supersede Tate & Blake's Annulatus Zone (1876 : 168) whose index species had been misidentified. Recently Sylvester-Bradley (1958 : 67–68) has shown that *Ammonites annulatus* J. Sowerby is a *Catacoeloceras* of the Bifrons Zone. The Tenuicostatum-Semicelatum Zone of Maubeuge (1948 : 59 ; 1957 : 189) and the Semicelatum Zone of Maubeuge (1952 : 365) are synonyms. Includes the upper part of the Acanthus Zone of Collenot (1869 : 172), the Zone of *Harpoceras schroederi* and *Lytoceras siemensi* of Denckmann (1893), Bode (1905) and Stolley (1909), and the *helianthoides*, *directus*, *Tiltoniceras* and *tenuicostatus* hemerae of Buckman (1930 : 41).

STRATIGRAPHY. The base of the zone is drawn at the first appearance of *Dactylioceras* in abundance after the disappearance of *Pleuroceras*, and in some areas in Britain this coincides with the appearance of *Tiltoniceras acutum* (Tate). The top is limited by the appearance of *Elegantuliceras* and *Harpoceras*.

In the type area of Yorkshire the zone comprises the stratigraphical division the Grey Shales, which is about 30 ft. thick. Careful collecting in the Grey Shales has enabled four horizons to be recognized as follows (kindly supplied in advance of publication by Prof. P. C. Sylvester-Bradley) :

4. *Dactylioceras semicelatum* horizon
3. *D. tenuicostatum* horizon
2. *Dactylioceras* sp. nov. horizon
1. Unfossiliferous beds (1 specimen of *Protogrammoceras* found)

These horizons have not yet been recognized anywhere else in the province. In Lincolnshire the zone consists of 15 ft. of shales, but farther south in the Midlands it is much thinner.

In parts of Oxfordshire, Leicestershire and Lincolnshire the base of the Tenuicostatum Zone is marked by a Transition Bed containing two characteristic ammonites, *Tiltoniceras acutum* and *Dactylioceras directum* (Buckman). This was called the *acutum* hemera by Buckman (1898, Table I, p. 450) and the Acutum Zone by Walford (1899 : 33). It is probably equivalent to the lowest horizon in the Grey Shales of Yorkshire and there is some evidence that it is present in the Junction Bed of the Dorset coast (*At* layer, Jackson, 1926 : 497–498). However, the limited geographical distribution of *Tiltoniceras acutum* does not warrant the separation of an Acutum Subzone.

In other British areas the Tenuicostatum Zone has not been separated, but it cannot be more than 2 or 3 ft. thick anywhere.

The zone has been recognized in exposures and borings over much of the Paris basin, eastern France, and Luxemburg, where the characteristic species of *Dactylioceras* are very common (Maubeuge, 1948, 1952, 1957 ; Mouterde, 1953 : 416 ; Collenot, 1869 ; Carré, 1876). At Bettembourg the thickness reaches 15–16 ft., and at many other places it is 10 ft. thick. The terms Semicelatum Zone and Semicelatum-Tenuicostatum Zone have been widely used in France, but both are junior synonyms of the correct name, Tenuicostatum Zone. The upper part of the " Acanthus Zone " of Collenot (1869 : 172) probably belongs to the Tenuicostatum Zone, but the exact horizon of *Dactylioceras acanthus* (d'Orbigny) is not known. *Tiltoniceras* has not been found in France or Luxemburg.

In north Germany the zone is known from boreholes to be at least 16 feet thick. From these and several surface exposures *Tiltoniceras schroederi* (Denckmann) and characteristic Tenuicostatum Zone species of *Dactylioceras* have been obtained (Hoffmann & Martin, 1960). This was Denckmann's horizon (1893) of *Harpoceras schroederi* and *Lytoceras siemensi*, which was used as a zone by Stolley (1909). In Swabia the zone is also present but probably much thinner, and the ammonites have yet to be collected in detail (Hoffmann & Martin, 1960 : 136).

FALCIFER ZONE

(Pl. 72, fig. 3)

Index species. *Harpoceras falcifer* (J. Sowerby, 1820 : 99, pl. 254, fig. 2). The holotype was figured by Buckman (1928, pl. 764).

Nomenclature. Oppel (1856 : 197) first suggested that *Ammonites serpentinus* Reinecke might form a better index species for his zone of *Posidonia bronni*, although he continued to use the latter. The Serpentinus Zone was subsequently restricted by the recognition of the Bifrons Zone above and the Tenuicostatum Zone below. Haug (1885 : 619) first proposed that *Harpoceras falcifer* be used as the index species instead of *H. serpentinum* on the grounds that most of the records of the latter were misidentifications of *H. falcifer*. Buckman and Arkell both accepted *H. falcifer* as the zonal index, but Spath (1942) reverted to *H. serpentinum* for reasons of priority. However, with the establishment of *H. falcifer* as the type species of *Harpoceras* and the reference of *Ammonites serpentinus* to the genus *Hildaites*, it is clear that *H. falcifer* is the only satisfactory zonal index, for *Harpoceras* is the characteristic genus of the zone.

STRATIGRAPHY. The zone corresponds to the combined stratigraphical ranges of the genera *Elegantuliceras* and *Harpoceras*. The only record of *Harpoceras* occurring in the Bifrons Zone above is Mouterde's *H. falcifer* (1953 : 417), claimed to occur in beds also yielding *Hildoceras bifrons* in eastern France, but in the absence of a figured specimen this cannot be checked, and it may be due to condensation. Several species of *Dactylioceras* and allied genera are present throughout the zone.

The subzones discussed below have been determined from the sequence in Britain. In North Germany several smaller divisions have been proposed which can be correlated exactly with the succession in Yorkshire. In Swabia and France the subzones have not been separated, but the zone as a whole and the characteristic ammonites are well developed, particularly in the *Posidonia* Shales of the Swabian Alb.

Exaratum Subzone

(Pl. 72, fig. 2)

INDEX SPECIES. *Harpoceras exaratum* (Young & Bird, 1828 : 266). The holotype was figured by Buckman (1909, pl. 5).

NOMENCLATURE. Introduced by Buckman (1910 : 86, 88 ; 1910*a* : xvi) as a zone between the Tenuicostatum and Falcifer Zones. It was relegated to a subzone of the Falcifer Zone by Arkell (1933) and Spath (1942). The Latescens Zone of Thompson (1910 : 462–463) is a synonym. It was based on the misidentification of a *Hildaites*, because *Ammonites latescens* Simpson is now known to be a *Pseudogrammoceras* of the Struckmanni Subzone in Yorkshire (Buckman, 1913, pl. 79 ; Dean, 1954 : 168). The zones of *Harpoceras capillatum*, *Harpoceras elegans*, and *Harpoceras boreale* used by Denckmann (1893), Bode (1905) and Stolley (1909) are synonyms.

Includes the *Elegantuliceras*, *Eleganticeras*, Grantham Ammonite, *exaratum*, *Harpoceratoides* and *crassoides* hemerae of Buckman (1930 : 39–40).

STRATIGRAPHY. The subzone corresponds to the combined stratigraphical ranges of *Elegantuliceras* and *Harpoceras exaratum*. In Yorkshire it consists of the Jet Rock, 25 ft. thick, and these ammonites occur in the following sequence :

2. *Harpoceras exaratum* and spp.
1. *Elegantuliceras* spp.

Species of *Hildaites* and *Harpoceratoides*, and *Monestieria erratus* (Simpson) also occur, mainly in the upper horizon. The latter species was wrongly referred to the genus *Pseudolioceras* by Buckman (1920*a*, pl. 188) ; the earliest British *Pseudolioceras* occurs in the Fibulatum Subzone.

At Grantham 15 ft. of shales contain *H. exaratum* and an undescribed species of *Elegantuliceras* (Buckman's " Grantham Ammonite "), but information as to the stratigraphical relation of these two species is lacking. In the Junction Bed of Dorset those layers yielding species of *Harpoceratoides* probably belong to this subzone. In other British areas, e.g. in the Stowell Park Borehole (Spath, 1956 : 143), the horizons in Yorkshire are not known to be separable, but the subzone as a whole is widely distributed and recognizable.

In Lower Saxony, North-west Germany, the lower part of the Upper Lias contains four layers of calcareous nodules in 4–5 ft. of shales, overlying 2 ft. of unfossiliferous beds on top of the Middle Lias. Ammonites obtained from the nodules led to the establishment of the following sequence of horizons by Denckmann (1887, 1893 : 109) and Bode (1905 : 219–220), used later as zones by Stolley (1909 : 287), Kumm (1941 : 236, 262–264) and Hoffmann (1949 : 115) :

4. Horizon of *Hildaites borealis* (Seebach)
3. Horizon of *Elegantuliceras* " *elegans* (Sowerby) " as figured by Denckmann (1887 : 58, pl. 4, fig. 5)
2. Horizon of *Elegantuliceras capillatum* (Denckmann)
1. Horizon of *Tiltoniceras schroederi* (Denckmann) and *Lytoceras siemensi* (Denckmann)

Horizon 1 belongs to the Tenuicostatum Zone and has been discussed above (p. 477). The position of *Harpoceras exaratum* is not clear, but from Bode's description of the succession (1905 : 219–220) it probably occurs in the shales between horizons 3 and 4, and in the 2–3 ft. of shale overlying horizon 4. In addition *Polyplectus subplanatus* (Oppel) and *Monestieria goslarensis* (Schloenbach) occur in horizon 4, and species of *Dactylioceras* occur throughout. This succession is exactly the same as that found in Yorkshire, and the sequence of *Elegantuliceras* followed by *Harpoceras exaratum* seems to be well established in the Yorkshire–North German basin.

Falcifer Subzone

(Pl. 72, fig. 3)

INDEX SPECIES and NOMENCLATURE. See Falcifer Zone. The use of the same index for both zone and subzone is unavoidable in this case. Synonyms are the Ovatum (or Pseudovatum) Zone of Buckman (see below) and the zone of *Harpoceras capellinum* of Denckmann (1893) and Stolley (1909). Includes the *crenatum, murleyi, anguiformis, anguinum, Hildaites, falciferum, tardum, facula, metorchion, Hildoceratoides, Harpocerate, pseudovatum, vermis* and *lobatum* hemerae of Buckman (1930 : 39–40).

STRATIGRAPHY. The lower limit is drawn at the first appearance of *Harpoceras falcifer*, which is not known to overlap with *H. exaratum*, and the top is limited by the appearance of *Hildoceras bifrons*.

In Yorkshire the subzone consists of the Bituminous Shales, containing the index species throughout, together with the overlying Ovatum Band, in all about 70 ft. of beds. Buckman (1910 : 85–87) introduced *Ammonites ovatus* Young & Bird, 1828 *non* 1822, as a zone index for the Ovatum Band. Later Buckman (1910*a* : xvi) substituted the name *pseudovatum*, which remained a *nomen nudum* until both the Young & Bird specimens were figured by Buckman in 1918 (1918*a*, pls. IIIA–C), and the genus *Ovaticeras* proposed. *Ovaticeras* is confined to the Ovatum Band in Yorkshire, and elsewhere it is very rare, being known only from a few specimens in the Midland counties. This distribution is too restricted for the recognition of an Ovatum Subzone.

In the Midlands and South-west England the subzone is developed almost everywhere in clay or Cephalopod Bed facies, and it is present in the Junction Bed of Dorset. Associations of *H. falcifer* and *Hildoceras bifrons* in some of the Cephalopod Beds are due to condensation, for these species are stratigraphically separate in the clay facies. Spath (1942 : 268) claimed that two horizons were recognizable : the upper with *Hildaites serpentinus* and the lower with *Elegantuliceras* sp. nov. (Buckman's " Grantham Ammonite "). This is not correct, for *H. serpentinus* is not known to characterize any particular horizon in the Falcifer Subzone, and Buckman's " Grantham Ammonite " comes from the Exaratum Subzone.

Orthildaites and *Hildaites* occur in this subzone, large specimens of *Hildaites serpentinus* (Reinecke), as interpreted by Buckman, and related species being particularly common in the Barrington–Ilminster area of Somerset. *Polyplectus subplanatus* (Oppel) has been recorded by Thompson (1910 : 464) from Northamptonshire and is the earliest record of this genus in Britain ; *Pseudolioceras lythense* (Young & Bird) recorded from Aveyron (Monestier, 1922 : 324) is the earliest *Pseudolioceras*.

Overlying the Exaratum Subzone (with its upper limit drawn 2–3 ft. above the horizon of *Hildaites borealis*) in Lower Saxony are 10–15 ft. of shales containing a hard marl band. These shales have been called the horizon of *Harpoceras capellinum* (Schlotheim) by Denckmann (1893 : 109) and Bode (1905) ; this was used later as a zone by Stolley (1909), Kumm (1941) and Hoffmann (1949). As well as *Polyplectus* [*Harpoceras*] *capellinus*, *Harpoceras falcifer* is very common, especially in the marl band, and *Hildaites serpentinus* (Reinecke), other species of *Hildaites*, and Dactylioceratidae also occur. This is clearly a Falcifer Subzone assemblage.

BIFRONS ZONE

(Pl. 72, fig. 4)

INDEX SPECIES. *Hildoceras bifrons* (Bruguière, 1789 : 40). The neotype (? holotype) was figured by Buckman (1918*a*, pl. 114A).

NOMENCLATURE. This species was first introduced as an index-fossil by Eudes-Deslongchamps (1864 : 74) for his " Couches à *Ammonites bifrons* et *serpentinus* " in Normandy. Reynès (1868 : 68) recognized the stratigraphical separation of these two ammonites and placed the " Zone à *A. bifrons* " between the Jurense Zone above and the " Serpentinus " Zone below.

The Commune Zone has long been used as a term synonymous with the Bifrons Zone. At its first introduction (Wright, 1858 : 25 ; 1863 : 53), however, the Commune Zone was made equivalent to Oppel's Bronni Zone (= Tenuicostatum + Falcifer + Bifrons Zones), and it was Tate & Blake (1876 : 16) who first restricted it to the beds between the Jurense and " Serpentinus " Zones. It is now known that the true *Dactylioceras commune* is restricted to the lower part of the range of *Hildoceras bifrons*, and in this sense it is used below as a subzonal index.

The Complanatus Zone of Collenot (1869 : 190) is a synonym ; it was used instead of the Bifrons Zone because *Hildoceras bifrons* was said to be rare in the area Collenot (1869 : 194–195) was describing.

STRATIGRAPHY. The zone corresponds to the stratigraphical range of *Hildoceras* (s.s.), i.e. excluding *Hildaites* and " *Hildoceratoides* " which occur earlier. The true *Hildoceras* is not known outside the zone.

All attempts at subdivision of the Bifrons Zone have been based largely on faunas of Dactylioceratidae, even though various genera of this family, and even *Dactylioceras* itself, range from the base of the Toarcian up to the Variabilis Zone. The divisions followed by Buckman, Spath and Arkell were introduced by Thompson (1910) ; these are accepted here, with the substitution of *Dactylioceras commune* as the index for the lowest subzone. The result is a scheme of three subzones founded on successive faunas of Dactylioceratidae and these have proved satisfactory at all places in the province where the succession is not too condensed for the faunas to be separated. Limitation of the top and bottom of the Bifrons Zone must still be based on the *Harpoceras-Hildoceras-Haugia* sequence.

The subzones can be applied in Yorkshire, the Midlands, a few places in South-west England, much of the eastern part of the Paris basin, and in Lorraine (Corroy & Gérard, 1933), but they have yet to be recognized in southern France (Aveyron), Swabia (where the *Posidonia* Shales belong partly to this zone) and North-west Germany.

Commune Subzone

(Pl. 72, fig. 5)

INDEX SPECIES. *Dactylioceras commune* (J. Sowerby, 1815 : 10, pl. 107, figs. 2, 3). The lectotype was figured by Arkell (1956, pl. 33, fig. 4).

NOMENCLATURE. It was introduced by Wright as " Communis-Bed " (1858 : 25) and used later as Communis Zone (Wright, 1863 : 53, 86). It was originally employed for all the Toarcian below the Jurense Zone, it was then used as an alternative index to *Hildoceras bifrons*, but it was finally abandoned by most workers as an index species in favour of the latter. Thompson (1910 : 464) used the alternative terms " Communis Beds, or Subcarinata Zone ", and thereafter *Frechiella subcarinata* was accepted as a subzonal index. The reasons for reverting to *D. commune* are first, priority, secondly, all the subzones of the Bifrons Zone are now based on Dactylioceratidae, and thirdly, *Frechiella* is always rare, and is therefore not suitable for a subzonal index.

It includes the *subcarinata*, *athleticum* and *bifrons* hemerae of Buckman (1930 : 39).

STRATIGRAPHY. The subzone corresponds to the range of *D. commune* and *D. athleticum* (Simpson), limited at the top by the incoming of species of *Peronoceras*. Other species and genera of Dactylioceratidae occur, but none with the distinctive ribbing of *Peronoceras*. No authentic records of *D. commune* are known from beds higher than the Commune Subzone, though closely related species of *Dactylioceras* do occur higher. *Hildoceras bifrons* is abundant, but the genera *Hildaites*, *Harpoceratoides* and *Harpoceras* are no longer present. All records of the latter genus prove to be *Polyplectus*.

Owing to the abundance of the index species the subzone is widely recognizable in Britain and France. In Yorkshire *D. commune* and *D. athleticum* range from the Hard Shales overlying the Ovatum Band up to the appearance of *Peronoceras*, giving a thickness of about 45 ft. The thickness is similar in the north Midlands. To the south-west the subzone has not been separated, although the index species occurs widely. In Somerset and Dorset it is represented in Junction and Cephalopod Beds.

South and east of the Paris basin and in Lorraine *D. commune* occurs abundantly and the subzone attains considerable thickness (Mouterde, 1953 : 417 ; Corroy & Gérard, 1933 : 200–201). In North Germany the subzone has not been separated, although *Frechiella brunsvicensis* Stolley occurs in the lower part of the Bifrons Zone (Hoyer, 1904 : 387–389).

Fibulatum Subzone

(Pl. 73, fig. 2)

INDEX SPECIES. *Peronoceras fibulatum* (J. de C. Sowerby, 1823 : 147, pl. 407, fig. 2). A topotype was figured by Buckman (1926, pl. 683).

NOMENCLATURE. Introduced by Thompson (1910 : 462). The subzone of *Porpoceras subarmatum* of Corroy & Gérard (1933 : 200) is a synonym.

STRATIGRAPHY. Corresponds to the range of *Peronoceras*, being limited at the top by the first appearance of *Zugodactylites*. Both thin-whorled and thick-whorled (" *Porpoceras* ") species of *Peronoceras* occur and also species of *Dactylioceras* (but not *D. commune*) and *Catacoeloceras*. *Hildoceras bifrons* is common and in this subzone the first British *Pseudolioceras* occurs, *P. lythense* (Young & Bird).

The thickest development of this subzone is 76 ft. of clay in Northamptonshire. It can also be separated at Grantham (Trueman, 1918 : 107) and in Yorkshire (Dean, 1954), but it has yet to be recognized in South-west England. In eastern France Mouterde (1953) did not separate it from the overlying Braunianus Subzone, although it is well developed and fairly thick in Lorraine where Corroy & Gérard (1933 : 201) recorded the characteristic *Peronoceras* fauna, and called it the subzone of *Peronoceras subarmatum*. It has yet to be recognized in Germany.

Braunianus Subzone

(Pl. 73, fig. 1)

INDEX SPECIES. *Zugodactylites braunianus* (d'Orbigny, 1845 : 327, pl. 104, figs. 1–3).

NOMENCLATURE. Introduced as used here by Thompson (1910 : 461). Previous uses of this ammonite as the index for a stratal term at Aveyron by Reynès (1868), Nicklès (1907) and Monestier (1922) are discussed below. The subzone of *Coeloceras crassum* of Corroy & Gérard (1933 : 200) is a synonym in part, but it includes also ammonites of the Variabilis Zone.

Includes the *braunianus*, *vigoense*, ? *subplanatum* and *semipolitum* hemerae of Buckman (1930 : 38).

STRATIGRAPHY. The lower boundary is drawn between the latest *Peronoceras* and the earliest *Zugodactylites braunianus*, and the upper boundary between the latest abundant *Hildoceras* and the earliest abundant *Haugia* and *Phymatoceras* faunas. In many areas *Z. braunianus* is characteristic of at least the lower part of the subzone. Species of *Catacoeloceras* are also common and characteristic, particularly in the higher part, but this genus is also common in the Variabilis Zone above. *Hildoceras bifrons* (including *H.* " *hildense* " Young & Bird sp.) and *H. semipolitum* Buckman are common in many areas, the latter species being confined to this subzone. Species of *Pseudolioceras* are also present. In several areas towards the south of the province a few *Haugia* and *Phymatoceras* appear in the upper half of this subzone while *Hildoceras* is still abundant, and similarly early examples are known in the Mediterranean Province. These are better regarded as rare forerunners of the Variabilis Zone Phymatoceratinae rather than abundant lingering *Hildoceras* faunas in the Variabilis Zone.

In Britain the index species is found only in Northamptonshire where it characterizes 70 ft. of clays. In Yorkshire the subzone is interpreted as comprising the beds between the highest *Peronoceras* and the lowest *Haugia*, and it includes the beds containing *Catacoeloceras* which were referred to the " Lilli Subzone " by Dean (1954 : 170–171) ; *H. bifrons* is present throughout. The lower part of the Cotswolds Sands contains *Hildoceras semipolitum* at levels consistently lower than the lowest *Haugia* and higher than *H. bifrons*, but Dactylioceratidae have yet to be found in these beds. At other localities in South-west England the Bifrons Zone is condensed in Junction Bed or Cephalopod Bed facies and this subzone is not separable.

In Lorraine Corroy & Gérard (1933 : 201–203) recorded a mixture of Braunianus Subzone and Variabilis Zone species from a phosphatic nodule bed above beds with *Peronoceras* ; this they called the subzone of *Coeloceras crassum*. In eastern France this subzone has not been separated from the Fibulatum Subzone, although in places the three ammonites *Hildoceras semipolitum*, *Zugodactylites braunianus* and *Catacoeloceras* sp. appear to be associated (Mouterde, 1953).

In the Aveyron district of southern France Reynès (1868 : 65–67) followed by Nicklès (1907 : 578–579) divided what they called the Bifrons Zone into three parts as follows (additions from Monestier's details (1922 : 324–327)) :

3. *Catacoeloceras crassum* (abundant), *Phymatoceras erbaense* (Hauer), *Dactylioceras* spp. and *Pseudolioceras* spp.
2. *H. bifrons* (abundant), *Phymatoceras erbaense* (rare), *Catacoeloceras crassum*, *Dactylioceras* spp. and *Pseudolioceras* spp.
1. *Z. braunianus*, *Peronoceras* spp., *Frechiella subcarinata*, *Catacoeloceras crassum*, *H. bifrons*, *Dactylioceras* spp., *and Praehaploceras zwieselei* (Monestier)

Many of these ammonites were figured by Monestier (1931), though unfortunately not those referred to as *H. bifrons*. *Z. braunianus* was said to be characteristic of division 1 and this was called the " Braunianum Subzone " by Monestier (1922 : 326) ; but it is clear from the list of species that division 1 contains almost the whole of the Bifrons Zone, and therefore Monestier's use of the term " Braunianum Subzone" is a synonym of Bifrons Zone. Division 2 contains abundant *Hildoceras* (recorded as *H. bifrons*, but they may well be *H. semipolitum*) together with *Catacoeloceras* and rare early *Phymatoceras*; this is the upper half of the Braunianus Subzone. Division 3, in which *Hildoceras* is no longer present but *Phymatoceras* fairly common, belongs to the Variabilis Zone.

This subzone has not been recognized in Germany.

UPPER TOARCIAN OR YEOVILIAN SUBSTAGE

VARIABILIS ZONE

(Pl. 73, fig. 4)

INDEX SPECIES. *Haugia variabilis* (d'Orbigny, 1845 : 350, pl. 113, figs. 1–4).

NOMENCLATURE. First used by Buckman (1888 : 45, 46, 50) as a subzone within the Jurense Zone, underlain by the Bifrons Zone. It was later employed by Welsch (1903 : 821) as a zone but has since reverted to a subzone constituting the basal subdivision of the Jurense Zone (Spath, 1942 : 265). Synonyms are: Mucronatus Zone of Collenot (1869 : 190); Buckman's (1925 : 75) Haugian Age, comprising the *lilli*, *malagma*, *variabilis*, *grandis* and *pauper* hemerae; Variabilis Zone plus Lilli Zone of Arkell (1930, Table facing p. 410); Variabilis-Schichten of Krumbeck (1943 : 281). The zone includes both "Banke des *Harpoceras doerntense* und *H. navis*" and "Banke des *Harpoceras illustre*" (Denckmann, 1893 : 109), names which were used later as zones by Stolley (1909).

STRATIGRAPHY. The lower limit of the zone is defined by the appearance of Phymatoceratinae in abundance, especially *Haugia* which is abundant throughout the zone, and the upper limit is drawn immediately below the first occurrence of *Grammoceras*. The incoming of the Phymatoceratinae coincides with the disappearance of *Hildoceras* in Britain, though the two are occasionally found together in the upper half of the Braunianus Subzone in some areas of France.

The fauna is well developed throughout the province and includes, in addition to *Haugia*, ammonites previously referred to *Denckmannia*, *Lillia* and *Pelecoceras*. All these are now placed in *Phymatoceras* or its subgenus *Chartronia* (Donovan, 1958 : 54; see also rejection of "Lilli Subzone" earlier in this paper, p. 475). The last Dactylioceratidae occur in this zone, species of *Dactylioceras* and *Catacoeloceras*, especially forms resembling *C. crassum* (Young & Bird), being very common at some localities in Swabia (Krumbeck, 1944 : 3) and at Aveyron (see p. 483). In Britain similar Dactylioceratidae are present in some exposures of the Variabilis Zone in the lower Cotswolds Sands (Buckman, 1889 : 444), but in Yorkshire they have not been found higher than the Braunianus Subzone, in strata which were previously assigned to the "Lilli Subzone" by Dean (1954 : 177). Other genera present include the long-ranging *Pseudolioceras*, and in Yorkshire the middle of the zone marks the upper limit of *Phylloceras heterophyllum* (J. Sowerby) (Dean, 1954 : 170). The genus

Whitbyiceras, type-species *W. pingue* (Simpson), was assigned by Buckman (1913 : 80*b*) to the Variabilis Zone on account of its supposed relationship to *Brodieia* [= *Brodiceras*]. *Whitbyiceras pingue* belongs, however, to the Harpoceratinae and was originally described from the Exaratum Subzone, whereas *Brodieia* is a characteristic member of the Phymatoceratinae from the Variabilis Zone in the Cotswolds and Somerset, and is also recorded widely elsewhere in Europe.

In Britain fossiliferous developments are found in the Peak Shales of Yorkshire, the lower Cotswolds Sands of the Cotswolds, and in condensed limestone sequences in Somerset and Dorset. The zone is absent throughout the Midlands.

In north-western Germany the term " *Variabilis* Bank " used by Engel (1894 : 55) has been shown by Ernst (1924, Table facing p. 118) to have its upper limit below that of the Variabilis Zone. The three zones of, successively, *Lillia robusta*, *Harpoceras doerntense* and *Haugia illustris* used by Ernst (1924) and since repeated by Kumm (1941) are together equivalent to the Variabilis Zone.

At Heiligenstein, Alsace, Schirardin (1914 : 343) proposed a " Zone der *Harpoceras bicarinatum* Zieten " which, from its position between what would here be called the Falcifer and Thouarsense Zones, might be considered to be partly equivalent to the Bifrons Zone. The zone was subdivided into two parts, also termed zones, a lower of *Lillia lilli* and an upper of *Haugia variabilis*. The latter appears to contain ammonites of both the Variabilis and Thouarsense Zones, but the former is more difficult to place. Several of the determinations are suspect and include genera normally found as high as the Levesquei Zone, but the large number of Phymatoceratinae recorded suggests that probably nothing more than part of the Variabilis Zone is represented. The Bifrons Zone is probably absent or condensed, and a phosphate bed with fossil débris has been recorded from this point in the succession by Theobald & Maubeuge (1950 : 274).

At Semur Collenot (1869 : 190) used Zones of *Ammonites complanatus*, *Turbo subduplicatus* and *Ammonites mucronatus*, successively overlying the Zone of *Ammonites serpentinus*. It has already been shown (p. 480) that the Zone of *A. complanatus* is equivalent to the present Bifrons Zone, but as the fauna listed (Collenot, 1869 : 199) includes *Ammonites erbaensis* von Hauer (now placed in *Phymatoceras*) the Variabilis Zone may be partly represented, though little is known of the overlap between *Hildoceras* and the Phymatoceratinae in France. The remaining zones of *Turbo subduplicata* and *A. mucronatus* together probably represent nothing higher than the Variabilis Zone as the former horizon contains *Haugia variabilis* (d'Orbigny) and the latter contains *Hammatoceras insigne* (Schübler), *Pseudolioceras lythense* (Young & Bird) and " *Dactylioceras* " *mucronatum* (d'Orbigny).

In France the " Zone à *Harpoceras bicarinatum* " used by Monestier (1921 : 281) at Aveyron occurs below the Thouarsense Zone ; the recorded fauna includes *Haugia*, *Lillia* and " *Dactylioceras* " (? misidentified as *Peronoceras*). South-east of Aveyron the " Zone à *Haugia variabilis* et *Harpoceras bicarinatum* " (Monestier, 1922 : 324) may be equivalent to the Variabilis Zone, but further work is necessary to establish the vertical range of the Phymatoceratinae in this area. At Poitiers the " Zone à *Pseudogrammoceras striatulum* " as used by Gillard (1940 : 601) apparently includes both the Variabilis Zone and the Striatulum Subzone.

THOUARSENSE ZONE

(Pl. 73, fig. 3)

Index species. *Grammoceras thouarsense* (d'Orbigny, 1844 : 222, pl. 57). An English specimen from the Cotswolds has been figured by Buckman (1928, pl. 774).

Nomenclature. The name was first used by Brasil (1895 : 39) in Normandy as " Niveau de *Grammoceras toarcense* (*sic*) et *G. fallaciosum* ", a term later modified to " Zone à *Grammoceras toarcense* " (Brasil, 1896 : 147). Brasil's faunal list contains *Grammoceras metallarium* (Dumortier), a species now placed in *Phlyseogrammoceras*, and the horizon may therefore include part of the Dispansum Subzone. Welsch (1911 : 9) has used " Zone à *Ammonites toarcensis* " in much the same sense as at present. Synonyms include : *Striatulum*-Beds (Buckman, 1890*a* : 77) ; Bank der *Harpoceras striatulum* (Denckmann, 1893) ; *striatuli* hemera as used by Buckman & Wilson (1896 : 687) ; Zone der *Harpoceras striatulum* (Stolley, 1909). Buckman's (1925 : 75) Grammoceratan Age comprises the Thouarsense Zone together with the overlying Dispansum Subzone.

Stratigraphy. The lower limit of the zone is defined by the sudden appearance of *Grammoceras*, particularly *G. striatulum* (J. de C. Sowerby) and *G. thouarsense*. The two species are closely related and frequently occur together, but in France *G. thouarsense* has also been recorded as coexisting with *Pseudogrammoceras* (s.s.), presumably in the Struckmanni Subzone (Gillard, 1940 : 603), and would appear to be a suitable zonal index, though it is not certain whether it ranges throughout the entire zone. Coincident with the appearance of *Grammoceras* is the disappearance of most of the Phymatoceratinae, at least in Britain, although the group continues upwards into the Striatulum Subzone as *Esericeras eseri* (Oppel), a species which has sometimes been referred to *Haugia*. The upper boundary of the zone is marked by the appearance of *Phlyseogrammoceras*.

Striatulum Subzone

(Pl. 74, fig. 3)

Index species. *Grammoceras striatulum* (J. de C. Sowerby, 1823 : 23, pl. 421, fig. 1). The holotype was refigured by Buckman (1890, pl. 26, figs. 7, 8).

Nomenclature. The name was first used by Hudleston (1874 : 295) as *Striatulus*-Beds, and later, as a subzone of the Jurense Zone, by both Buckman (1888 : 45, 50 ; 1890*a* : 76–80) and Spath (1942 : 265). Synonyms include : *eseri* hemera (Buckman, 1925 : 75) ; Striatulum Zone (Arkell, 1930, Table facing p. 410) ; Eseri Zone (Gillard, 1940 : 602) ; *Toarcensis*-Schichten (Krumbeck, 1943 : 281).

Stratigraphy. The base of the subzone is defined by the appearance of the first *Grammoceras*, and it ends with the incoming of *Pseudogrammoceras*. In the lower part of the Striatulum Shales in Yorkshire the zonal ammonite is accompanied by other species of *Grammoceras*, together with the characteristic *Pleurolytoceras* ? *gubernator* (Simpson). *Pseudolioceras* is fairly common, particularly *P. compactile* (Simpson) for which this is the type horizon. Elsewhere in England the subzone is found only in the Cotswolds, Somerset and Dorset where it usually occurs either as sandstones, part of the Midford Sands and Cotswolds Sands, or within a condensed sequence. These outcrops contain the only recorded English specimens of *Esericeras eseri* (Oppel), but the species is widely recorded elsewhere in Europe.

In Scotland the Raasay Ironstone of the Hebridean area was at one time thought to belong to the Bifrons Zone (Buckman, 1920 : 67) owing to its containing " *Hildoceras bifrons* (d'Orbigny *non* Bruguière) ", but as the result of additional evidence from the Ardnamurchan district the age was redetermined as " Striatulum Zone " and the Whitbian ammonites which were also present were described as being derived (Buckman *in* Richey & Thomas, 1930 : 43–44). The fossils upon which this claim was founded were obtained from loose blocks of ironstone near Kilchoan, and we are indebted to Mr. R. B. Wilson of the Geological Survey of Scotland for the loan of these specimens. Although no information is available regarding the original position of the fossils within the rock, the ammonites appear to belong to two distinct horizons. The lower is represented mainly by Dactylioceratidae indicating the Bifrons Zone, though no *Hildoceras* is present ; the higher is shown to be Thouarsense Zone by two specimens of *Grammoceras*. The condition of the Dactylioceratidae of the Bifrons Zone suggests that they are indigenous, and not derived as claimed by Buckman. It seems likely that parts of both the Bifrons and Thouarsense Zones are represented, with a stratigraphical break between them occurring within the Ironstone. A further break occurs between the Ironstone and the overlying Dun Caan Shales which belong to the Aalensis Subzone.

In France the " Zone à *Haugia eseri* " used by Gillard (1940 : 602) at Poitiers was said to overlie a " Striatulum Zone ", though the two were difficult to separate in some places. The fauna listed by him includes several Phymatoceratinae, such as *Denckmannia*, *Haugia* and *Phymatoceras*, which are characteristic of the Variabilis Zone, and the sequence may be condensed.

Struckmanni Subzone

(Pl. 74, fig. 1)

Index species. *Pseudogrammoceras struckmanni* (Denckmann, 1887 : 72, pl. 3, fig. 1).

Nomenclature. The name was first used by Buckman (*in* Buckman & Wilson, 1896, footnote to p. 688) to denote a subdivision " 3. *Grammoceras Struckmanni*, and allied species ", and later as *Struckmanni* hemera (Buckman, 1898, Table facing p. 450). Since then the name has been generally used for a subzone of the Jurense Zone (Spath, 1942 : 265). Synonyms include : *dispansi* hemera as used by Buckman & Wilson (1896 : 700) ; *Pedicum* Bed (Richardson, 1910 : 106) ; Pedicum Zone (Buckman, 1912 : *c*) ; Struckmanni Zone (Arkell. 1930, Table facing p. 410) ; Fallaciosum Subzone (Muller, 1941, Table 2) ; *Fallaciosus*-Schichten (Krumbeck, 1943 : 281). The " Zone à *Ammonites insignis* " proposed by Welsch (1911 : 9) at Thouars includes both the Struckmanni and Dispansum Subzones.

Stratigraphy. The base of the subzone is defined by the appearance of *Pseudogrammoceras*, and the top is placed immediately below the first occurrence of *Phlyseo-*

grammoceras. *Pseudogrammoceras* has recently been placed in the synonymy of *Grammoceras* (Arkell *in* Arkell, Kummel & Wright, 1957 : L261) but the two are regarded here as being generically distinct ; they are found together in at least the lower part of the subzone. Most of the known British species of *Pseudogrammoceras* have been found in the condensed cephalopod-bed facies of the Cotswolds ; in the upper Striatulum Shales of Yorkshire the genus is uncommon, though *P. latescens* (Simpson) is characteristic (Dean, 1954 : 178). Arkell's (1933 : 171) claim, founded on the record of *Grammoceras fallaciosum*, a species now assigned to *Pseudogrammoceras*, that the Dispansum Subzone is present in Dorset is probably incorrect.

In France, south-east of Aveyron, Monestier (1921 : 283, 285) proposed a " Zone à *Pseudogrammoceras expeditum* Buckman ", overlain by the " Zone à *Polyplectus discoides* Zieten et *Hammatoceras insigne* Schübler ". These two zones are together probably equivalent to all, or part of, the Struckmanni Subzone.

The " Zone à *Grammoceras fallaciosum* " as used at Tournemire by Nicklès (1907 : 579) overlies the Bifrons Zone, the Variabilis Zone apparently being absent, and is in turn overlain by the " Zone à *Dumortieria radiosa* ". The recorded fauna includes *Pseudogrammoceras*, *Paroniceras sternale* (von Buch) and *Polyplectus* (= *Lioceras discoides*), and the zone probably comprises both the Struckmanni and Dispansum Subzones, though *Phlyseogrammoceras* is not recorded.

In Lorraine, Corroy & Gérard (1933) have employed the term " Zone à *Pseudogrammoceras fallaciosum* auct." in a broad sense, probably equivalent to the Striatulum to Dispansum Subzones of the present paper. Their faunal lists show that their successive horizons of *Pseudogrammoceras expeditum* and *Hammatoceras insigne* fall within the Struckmanni Subzone, but their record of *Frechiella subcarinata* (Young & Bird), a characteristic species of the Bifrons Zone, is probably a misidentification of a *Paroniceras*, for *P. sternale* (von Buch) is also recorded.

Although the " Horizon à *Hammatoceras insigne*, *Lytoceras germaini* et *Paroniceras sternale* " proposed by Piroutet (1920 : 21) near Salins, in the Jura, is underlain by strata with " *Grammoceras fallaciosum* " (now *Pseudogrammoceras*) its fauna appears to include both *Grammoceras* and *Pseudogrammoceras*, and the age of the stratum is probably Struckmanni Subzone. Of the supposed zonal indices, *Paroniceras sternale* has a long vertical range and has been recorded by Gillard (1940 : 602–603) from the Striatulum, Struckmanni and Dispansum Subzones. The same writer has distinguished two successive zones of *Pseudogrammoceras pedicum* and *P. struckmanni* at Poitiers (Gillard, 1940 : 603–604), but his faunal list suggests that the two are together equivalent to the present Struckmanni Subzone.

LEVESQUEI ZONE

(Pl. 73, fig. 5)

INDEX SPECIES. *Dumortieria levesquei* (d'Orbigny, 1844 : 230, pl. 60). Species figured by Roquefort & Daguin (1929, pl. 22, fig. 5).

NOMENCLATURE. First used by Benecke (1901 : 144, 149) as *Levesquei*-Schichten in the area of Lorraine and Luxemburg. Buckman's Dumortierian Age (1925 : 75), comprising the *Hammatoceras*, *levesquei*, *novata*, *subsolaris*, *Catulloceras* and *moorei* hemerae, together with the *dispansum* hemera from the preceding Grammoceratan Age, includes the Dispansum to Moorei Subzones inclusive. The *Levesquei*-Schichten of Krumbeck (1943 : 281) include the Levesquei to Aalensis Subzones. The Opalinum Zone as used by Wright (1879 : 163) probably includes the Moorei and Aalensis Subzones in addition to the Opalinum Subzone of the Bajocian, with his Jurense Zone comprising the Variabilis Zone to the Levesquei Subzone inclusive.

STRATIGRAPHY. The base of the zone is defined by the incoming of *Phlyseogrammoceras*, sometimes accompanied by *Dumortieria*, though not in Britain. The appearance of these genera coincides more or less with the extinction of *Pseudogrammoceras*, and the lower and upper limits of the zone mark the maximum recorded vertical range of *Dumortieria*. Three of the four subzones recognized here as constituting the zone are founded on closely-related forms, two species of *Dumortieria* with one of *Pleydellia*. It would have been preferable, if possible, to use another species of *Dumortieria* for the lowest subzone, but the genus is only known from this horizon in a few extra-British areas, whereas *Phlyseogrammoceras dispansum* and allied species are widespread and fairly abundant.

Dispansum Subzone

(Pl. 74, fig. 2)

INDEX SPECIES. *Phlyseogrammoceras dispansum* (Lycett, 1860 : 146). The species was figured for the first time, as *Harpoceras variabilis* var. *dispansum*, by Wright (1882, pl. 67, figs. 3, 4).

NOMENCLATURE. The name was first used by Buckman (1889 : 443) as *Dispansum*-Beds, apparently in the same sense as in the present paper, and has usually been employed as a subzone of the Jurense Zone (Spath, 1942 : 265). Synonyms include : *Hammatoceras* hemera (Buckman & Wilson, 1896 : 688) ; Dispansum Zone (Buckman, 1910 : 88) ; *dispansi* hemera (Buckman, 1910*a* : xvi) ; *Dispansus*-Schichten (Krumbeck, 1943 : 281) ; Sous-zone à *Hammatoceras insigne* (Theobald & Maubeuge, 1950 : 274). The stratigraphical position of the " Zone à *Dumortieria pseudoradiosa* " employed by Brasil (1896 : 147) at Calvados would apparently make it equivalent to the Dispansum to Moorei Subzones inclusive.

STRATIGRAPHY. The appearance of *Phlyseogrammoceras*, particularly *P. dispansum*, defines the base of the subzone, coinciding with the disappearance of *Pseudogrammoceras*. In Yorkshire the genus *Hudlestonia* is most common in this subzone. At one time Buckman (1911 : 210) suggested that in the Cotswolds a *Hudlestonia* horizon might possibly be present between what are now the Dispansum and Levesquei Subzones, but as the sequence there is condensed such a horizon would be difficult to prove and its existence is considered unlikely. *Hudlestonia* has been recorded from the Levesquei and Moorei Subzones of the Cotswolds and Somerset, whilst outside Britain the genus has been found in both the Moorei and Aalensis Subzones by Krumbeck (1943 : 281, 291). According to Denckmann (1897 : 21–22) the horizon of *Hudlestonia affinis* (Seebach), the type-species of the genus, is between the Aalensis and Opalinum Subzones.

The number of other ammonite genera in the British development of the subzone is small and includes only *Alocolytoceras* and *Hammatoceras*, but elsewhere in Europe the horizon marks the earliest appearance of *Dumortieria*. Species definitely recorded from the Dispansum Subzone include *D. insignisimilis* Brauns and *D. striatulocostata* (Quenstedt) in Swabia (Krumbeck, 1943 : 287, 316), but other forms, though recorded, are not specifically identified. Other characteristic ammonites include *Alocolytoceras* ? *peregrinum* (Simpson) and various species of *Phlyseogrammoceras* such as *P. metallarium* (d'Orbigny), *P. orbignyi* Buckman and *P. dispansiforme* (Wunstorf). Gillard's (1940 : 605) record of *Cotteswoldia distans* Buckman in association with *P. dispansum* at Poitiers probably refers to a species of *Dumortieria*.

To the south-east of Aveyron, Monestier (1921) employed the following four successive zones in the upper portion of the Upper Lias : *Grammoceras striatulum*; *Pseudogrammoceras expeditum*; *Polyplectus discoides* and *Hammatoceras insigne*; *Pseudogrammoceras reynesi* and *Phlyseogrammoceras dispansum*. Several of the ammonites were figured subsequently by Monestier (1921*a*) but many of the generic determinations are suspect and in need of revision. It is possible that the succession of zones and subzones present may not, in fact, range from Striatulum to Dispansum.

Levesquei Subzone

(Pl. 73, fig. 5)

Index species. See Levesquei Zone.

Nomenclature. The name as first used by Benecke (1901 : 149) was a subdivision which included also the equivalent of the Dispansum Subzone. It was first employed in the present sense by Buckman (1925 : 75) as the *levesquei* hemera, and has since been used as a subzone of the Jurense Zone (Spath, 1942 : 265). Synonyms include : *Dumortieria* Zone (Buckman, 1910 : 88 ; Arkell, 1930, Table facing p. 410) ; Subzone of *Dumortieria* spp. (Arkell, 1933 : 165) ; *Striatulo-costatus* Lage (Krumbeck, 1943 : 281).

Stratigraphy. In England the base of the subzone is defined by the first appearance of *Dumortieria* which, as far as is known, coincides with the extinction of *Phlyseogrammoceras*. The most fossiliferous English development is found in the Cotswolds, but the sequence there is condensed and exact horizons are difficult to distinguish. In Dorset the subzone is present either condensed, or as sandstones generally similar to those of Yorkshire, where the fauna has not yet been found.

Numerous species, probably too many, of *Dumortieria* have been described and, generally speaking, they can be said to fall into two groups which form the basis of subdivision of the middle portion of the Levesquei Zone. Although exceptional and transitional forms are known, the early species of *Dumortieria* tend to be coarsely ribbed, constituting what Ernst (1924 : 118) called the "*Levesquei*-Gruppe". The earliest-known species are recorded from the Dispansum Subzone, at which horizon, in North-west Germany, they include *Dumortieria sparsicosta* Haug and *D. munieri* Haug, and in Swabia *D. striatulocostata* (Quenstedt), together with an occasional record of *D. levesquei* itself (Corroy, 1931 : 205 ; Krumbeck, 1943 : 316). The amount of overlap between *Dumortieria* and *Phlyseogrammoceras* is small and individuals of the former genus become much more numerous after the extinction of the latter. The absence of *Phlyseogrammoceras* is an important factor in defining the base of the Levesquei Subzone, and the upper limit of the subzone is drawn immediately below the first appearance of *Dumortieria moorei* (Lycett) and allied forms. Species which appear to be particularly characteristic of the Levesquei Subzone include *Dumortieria levesquei*, *D. munieri*, *D. subsolaris* Buckman, *D. striatulocostata* and *D. prisca* Buckman.

The equivalents of the Levesquei and Moorei Subzones have sometimes been grouped together under one stratigraphical name, and these include : *Dumortieria*-Beds (Buckman & Wilson, 1896 : 707) ; *Dumortieriae* hemera (Buckman & Wilson, 1896 : 677) ; Zone à *Dumortieria radians* (Welsch, 1903 : 821 ; 1911 : 9–10) ; Zone à *Dumortieria* (Roquefort & Daguin, 1929 : 252) ; Subzone of *Dumortieria* spp. (Dean, 1954 : 166) ; and, perhaps, Sous-zone à *Dumortieria radiosa* (Theobald & Maubeuge, 1950 : 274). The " Zone à *Dumortieria radiosa* " used by Nicklès (1907 : 580) at Tournemire may include both the Levesquei and Moorei Subzones, but it is difficult to tell from his description. Another subdivision with *D. radiosa* as index used in Germany by Ernst (1924, Table facing p. 118), who was followed by both Kumm (1941 : 238) and Hoffmann (1949 : 115), apparently includes the Moorei Subzone together with an undetermined upper portion of the Levesquei Subzone. The " Zone à *Dumortieria levesquei* " as used in France, north of the Massif Central, by Mouterde (1953 : 7) is made up of successive horizons of *D. radiosa* (Seebach) and *D. moorei* ; it seems probable that the former, as employed by him, is equivalent to the Levesquei Subzone.

Moorei Subzone

(Pl. 74, fig. 5)

INDEX SPECIES. *Dumortieria moorei* (Lycett, 1857 : 122, pl. 1, fig. 2a. only). Holotype refigured by Wright (1884, pl. 80, figs. 1, 2).

NOMENCLATURE. The name was first used by Buckman (1889 : 443) as *Moorei*-Beds, and later as Moorei Zone (Buckman, 1910 : 88), since which time it has been reduced to a subzone of the Jurense Zone (Spath, 1942 : 265). Synonyms include : Zone à *Dumortieria radiosa* (Schneider, 1927 : 8) ; Moorei Zone (Arkell, 1930, Table facing p. 410) ; *Radiosus*-Schichten (Krumbeck, 1943 : 281). The subzone probably comprises the *novata*, *subsolaris*, *Catulloceras* and *moorei* hemerae of Buckman's (1925 : 75) Dumortierian Age.

STRATIGRAPHY. The base of the subzone is defined by the appearance of *Dumortieria moorei*, and the upper limit is drawn below the appearance in force of *Pleydellia aalensis* and allied forms. The latter appear to coincide with the disappearance of *D. moorei*, but other species of *Dumortieria* range upwards and may even include occasional records of coarsely-ribbed forms such as *D. costula* and *D. munieri* which form an uncommon exception to the general rule that the finely-ribbed and striate species are the stratigraphically younger. These records have been encountered in Swabia (Krumbeck, 1943 : 291, 295, 324) but in other areas *Dumortieria* is generally absent from the Aalensis Subzone. Most of the species of *Dumortieria* which are restricted, or nearly so, to the Moorei Subzone are finely ribbed and belong to the "*Radiosa*-Gruppe" of Ernst (1924 : 118); they include *D. moorei*, *D. radiosa* (Seebach), *D. pseudoradiosa* (Branco), *D. gundershofensis* Buckman and *D. rhodanica* (Haug).

In England the subzone is found in Yorkshire, constituting the uppermost Yellow Beds of the Blea Wyke Sands, and in the Somerset–Dorset and Cotswolds areas where it is present usually either as sandstones, the Ham Hill Stone and part of the Yeovil Sands, or in the condensed sequence of the cephalopod-bed facies. Most of the species of *Pleydellia* described by Buckman from the "Cephalopod-Bed" of the Cotswolds were said originally to have been collected from the Moorei Subzone, but their horizon was subsequently emended to Aalensis Subzone (Buckman, 1904 : cxxxvii–cxxxviii) and the genera *Pleydellia* and *Dumortieria* have yet to be discovered together in Britain. In addition to *Dumortieria*, other ammonites recorded from the Moorei Subzone in Britain include *Phylloceras* [*Xeinophylloceras*] *xeinum* (Buckman) and *Catulloceras* [*Dactylogammites*] *digitatum* (Buckman), the latter genus being found more abundantly in the Aalensis Subzone. Previous records suggest that *Pleurolytoceras leckenbyi* (Lycett) is probably confined to the Moorei and Aalensis Subzones.

On the Continent, in Lorraine, Benecke (1901 : 154) introduced a subdivision termed "Schichten der *Dumortieria subundulata* und des *Lioceras opalinum*", the lowest part of which, "das braune lager", is equivalent to the Moorei Subzone as it contains *D. moorei*, *D. pseudoradiosa* and *D. bleicheri* Benecke. The last-named species has been recorded only from this horizon in Swabia by Krumbeck (1943 : 286).

Aalensis Subzone

(Pl. 74, fig. 4)

INDEX SPECIES. *Pleydellia aalensis* (Zieten, 1832 : 37, pl. 28, fig. 3). An English specimen from the Cotswolds was figured by Buckman (1890, pl. 32, figs. 3–6).

NOMENCLATURE. The name was first used as "Zone à *Ammonites aalensis*" by Reynès (1868 : 68) for strata overlying the Jurense Zone. It was adopted by Buckman (1913 : x) for the English succession as the lowest subdivision of the "Aalenian Stage" and Inferior Oolite. He was followed by Arkell (1933 : 165), but Spath (1942 : 265), following the original definition of Toarcian and Aalenian, rightly retained it in the Toarcian Stage and used it as the topmost subzone of the Jurense Zone. Synonyms are numerous and include: Couches à *Ammonites torulosus* (Mayer-Eymar, 1864); *aalensis* hemera (Buckman & Wilson, 1896 : 677ff.); Zone à *Pleydellia* (Roquefort & Daguin, 1929 : 253); Aalensis Zone (Arkell, 1930, Table facing p. 410); *Hircinus*-Schichten and, probably, *Torulosus*-Schichten (Krumbeck, 1943 : 281, 293); Sous-zone à *Pleydellia aalense* et *Gotteswaldia* (*sic*, misprint of *Cotteswoldia*) *costulata* (Theobald & Maubeuge, 1950 : 274); Zone à *Lytoceras torulosum* (Theobald & Maubeuge, 1950 : 280); Zone à *Canavarina venustula*, Zone à *Gotteswaldia* (*sic*) *spathi*, Zone à *Dumortieria pseudoradiosa*, and Zone à *Pleydellia buckmanni* (Theobald & Maubeuge, 1950 : 282). The whole of Buckman's (1925 : 75) Canavarinan Age, comprising the *Cotteswoldia*, *digna*, *venustula* and *Canavarella* hemerae, is equivalent to the Aalensis Subzone.

STRATIGRAPHY. The base of the subzone is defined by the appearance of *Pleydellia aalensis* and allied species, whilst the top is drawn immediately below the first *Leioceras*. So far as is known the limits of the subzone are generally defined by the vertical range of *Pleydellia* in abundance, though the genus may occasionally range upwards into the basal Bajocian. Although Arkell (*in* Arkell, Kummel & Wright, 1957 : L261) has placed Buckman's genera *Canavarina*, *Canavarella*, *Cotteswoldia* and *Walkericeras* in the synonymy of *Pleydellia*, the names have been frequently employed and given at least subgeneric status, particularly by French palaeontologists. *Walkericeras subglabrum* Buckman has been recorded from the *opaliniforme* hemera of the Hebrides by Buckman (1920 : 66).

In France, north of the Massif Central, Mouterde (1953 : 7) has recognized a horizon of *Pleydellia mactra* (Dumortier) underlying that of *P. aalensis*, but it is doubtful whether such a separation is more than locally applicable and the two species have been recorded together at Thouars (Welsch, 1911 : 10), at Hérault, southern France (Roquefort & Daguin, 1929 : 253), and in Swabia (Krumbeck, 1943 : 294, 297). The ammonites of the " Zone à *Dumortieria moorei* et *Lioceras partitum* ", a subdivision in Lorraine proposed by Gérard & Bichelonne (1940 : 23), have been redescribed by Maubeuge (1946) as species of *Pleydellia* and *Cotteswoldia* belonging to the Aalensis Subzone.

The best development of the subzone in Britain is in the Dun Caan Shales of Raasay, where the ammonite fauna resembles that of the uppermost Yeovil Sands of Crewkerne, Somerset (Arkell, 1933 : 183). It was here that Buckman (1920) first established the *Cotteswoldia*, *digna* and *venustula* hemerae, horizons which are probably of no more than local significance. The subzone is not developed in Yorkshire, is found condensed in the Cotswolds, and is only thinly developed in Somerset and Dorset, mainly as the topmost Yeovil and Bridport Sands together with thin, overlying clays and limestones. *Pleurolytoceras hircinum* (Schlotheim) is widespread at this horizon and may be restricted to it. *Pleydellia* and *Dumortieria* are generally found at separate horizons but have been recorded together in Swabia (Krumbeck, 1943 : 294, 302), and in France north-east of the Massif Central (Mouterde, 1953 : 365).

VIII. INDEX TO STAGES, ZONES, SUBZONES AND HEMERAE

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PLATE 63

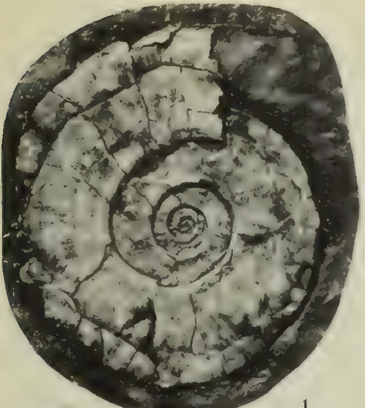
FIG. 1. *Psiloceras planorbis* (J. de C. Sowerby). Watchet, Somerset. Lectotype, figured by J. de C. Sowerby, 1824, pl. 448, upper figure. BM. 43875. × 1.

FIG. 2. *Psiloceras (Caloceras) johnstoni* (J. de C. Sowerby). Watchet, Somerset. BM. 67976. × ¾.

FIG. 3. *Alsatites liasicus* (d'Orbigny). Pouilly, Côte d'Or. Lectotype, figured by d'Orbigny, 1844, pl. 48, and by Reynès, 1879, pl. 6, figs. 9–12. Muséum d'Histoire naturelle, Paris, coll. d'Orbigny 1441. × ⅖.

FIG. 4. *Schlotheimia (Waehneroceras) portlocki* (Wright). Kaye's Quarry, Stockton, Warwickshire. BM. C8555. × ¾.

FIG. 5. *Alsatites laqueus* (Quenstedt). Bebenhausen, Württemberg. Holotype, figured by Quenstedt, 1856, pl. 3, fig. 5. Geol.-Pal. Institut, Tübingen, Ce 5/1/14. × 1.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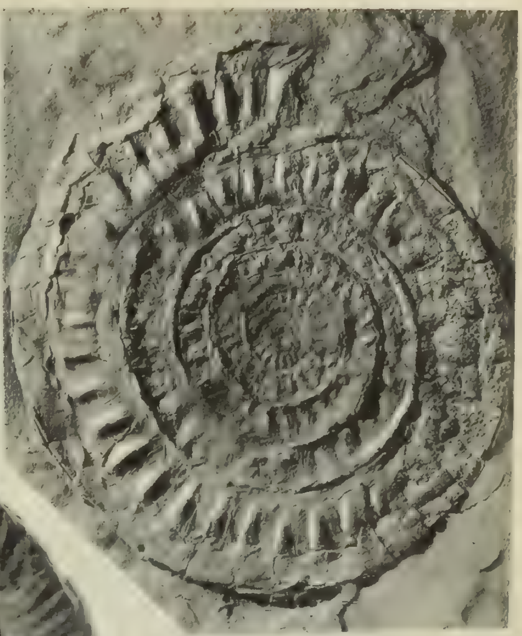
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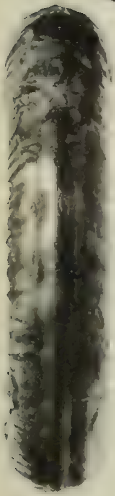
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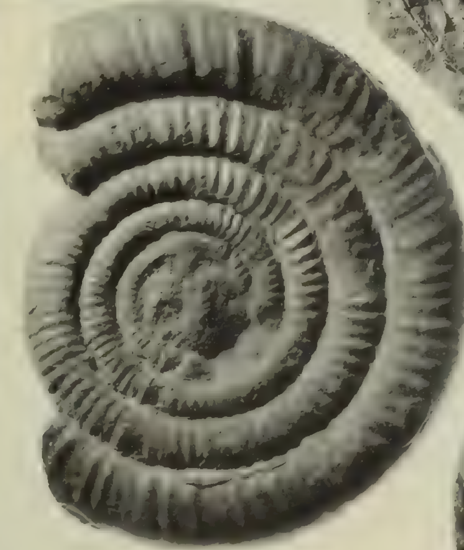
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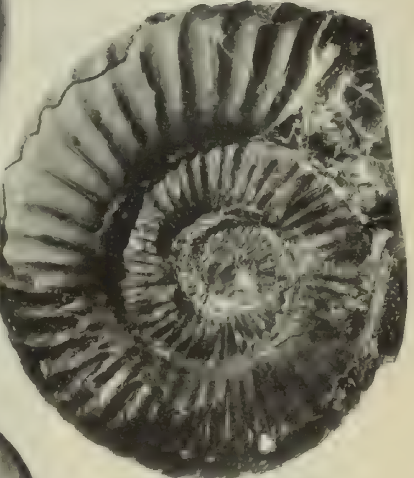
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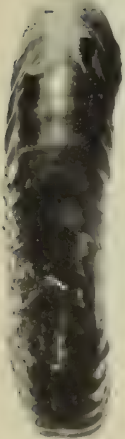
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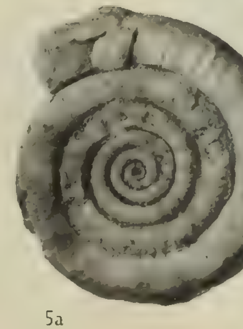
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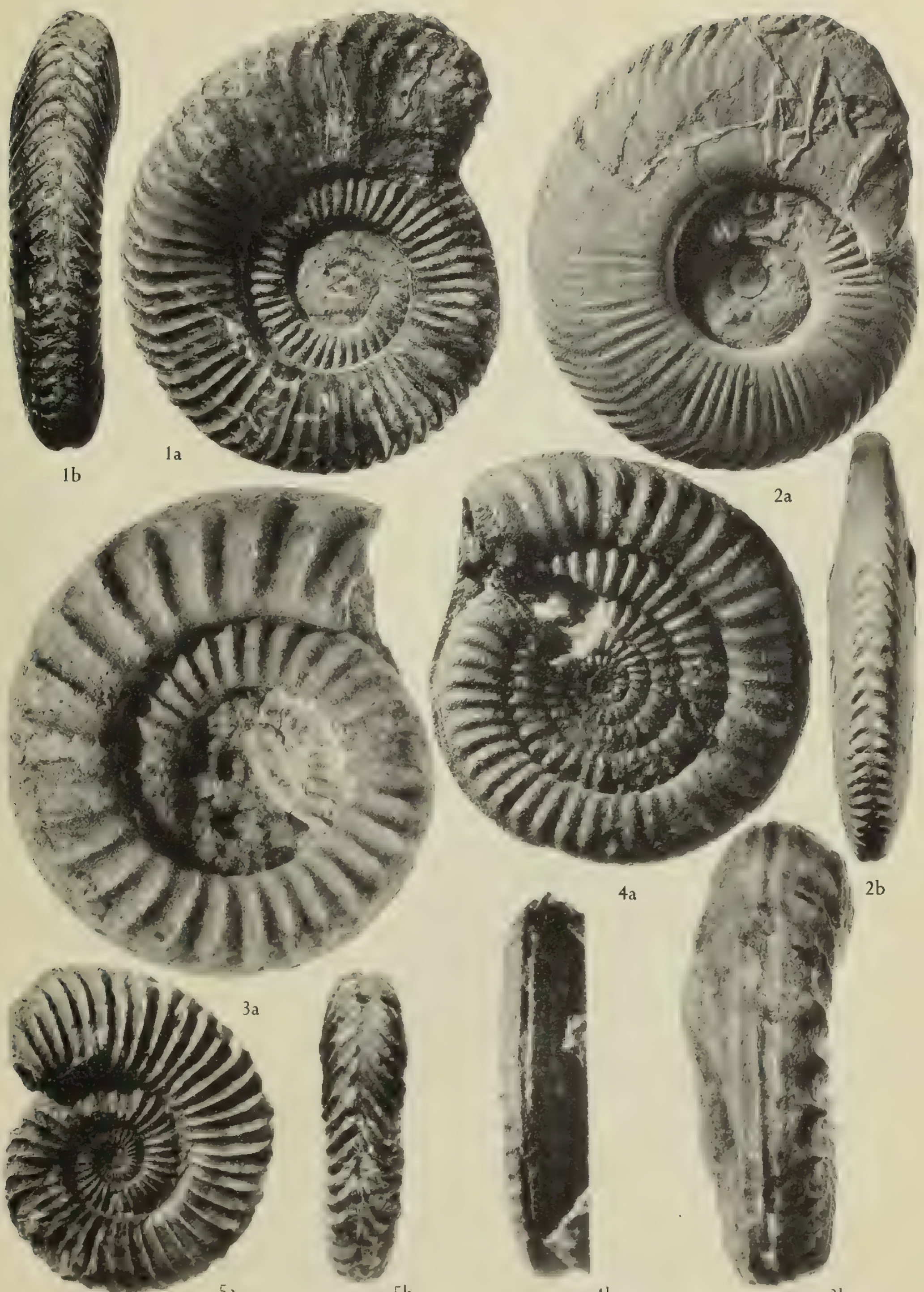
HETTANGIAN ZONAL AMMONITES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HETTANGIAN AND LOWER SINEMURIAN ZONAL AMMONITES

PLATE 65

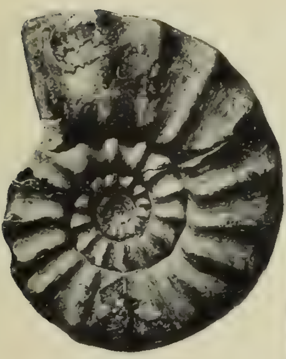
FIG. 1. *Euagassiceras sauzeanum* (d'Orbigny). Gloucestershire. BM. 39586. × 1.

FIG. 2. *Coroniceras rotiforme* (J. de C. Sowerby). Near Yeovil, Somerset. Holotype, figured by J. de C. Sowerby, 1824 : 76, pl. 453. BM. 43975. × ½.

FIG. 3. *Agassiceras scipionianum* (d'Orbigny). Robin Hood's Bay, near Whitby, Yorkshire. BM. 37909. × 1.

FIG. 4. *Arnioceras semicostatum* (Young & Bird). Robin Hood's Bay, near Whitby, Yorkshire. Referred to by Spath, 1923 : 70. BM. C25651. × 1.

FIG. 5. *Coroniceras reynesi* (Spath). Pittsville, Keynsham, Somerset. Bristol University, Geology Dept., 211. × ⅔.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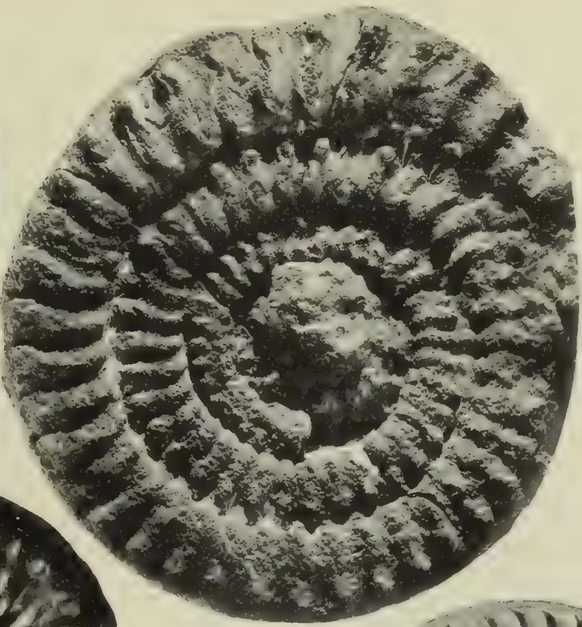
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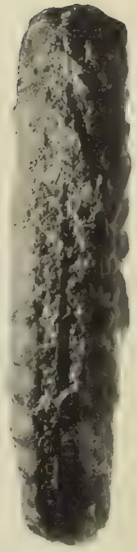
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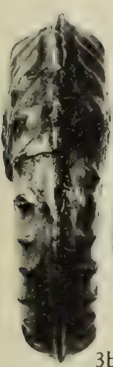
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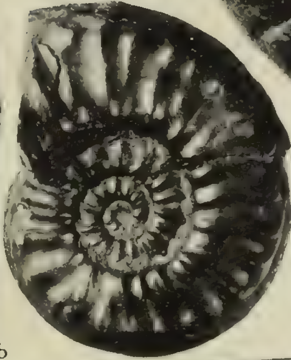
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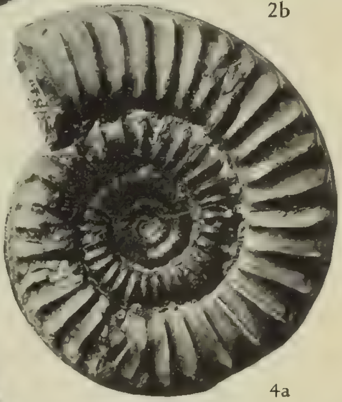
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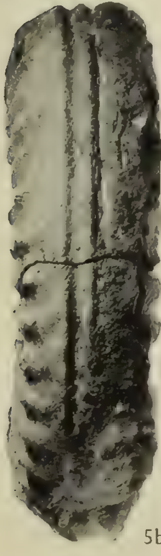
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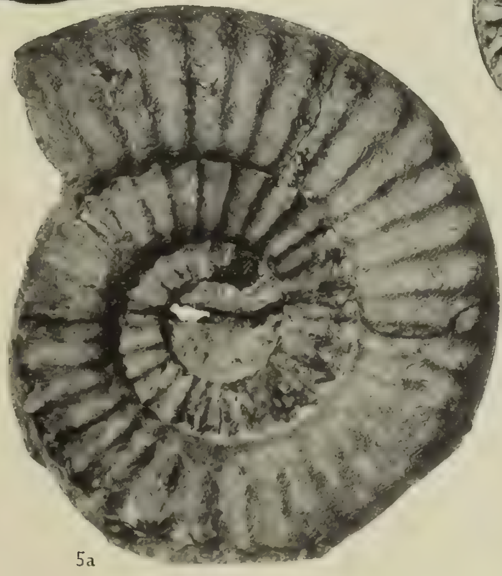
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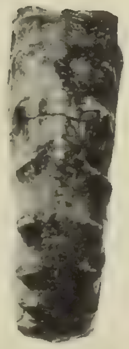
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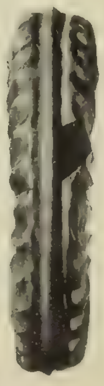
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LOWER SINEMURIAN ZONAL AMMONITES

PLATE 66

FIG. 1. *Caenisites brooki* (J. Sowerby). Charmouth, Dorset. BM. C56066. × ¾.

FIG. 2. *Caenisites turneri* (J. de C. Sowerby). Bredon Hill, Worcestershire. BM. 67979. × 1.

FIG. 3. *Microderoceras birchi* (J. Sowerby). Charmouth, Dorset. BM. 67973. × 1.

FIG. 4. *Eparietites denotatus* (Simpson). Robin Hood's Bay, near Whitby, Yorkshire. Figured (as *Eparietites impendens* (Young & Bird)) by Tate & Blake, 1876 : 290, pl. 6, fig. 7. BM. C17936. × 1.

FIG. 5. *Oxynoticeras oxynotum* (Quenstedt). Schömberg, Württemberg. Holotype, figured by Quenstedt, 1845 : 98, pl. 5, fig. 11, and Quenstedt, 1884 : 175, pl. 22, fig. 29. Geol.-Pal. Institut, Tübingen, Ce 5/22/29. × 1.

PLATE 64

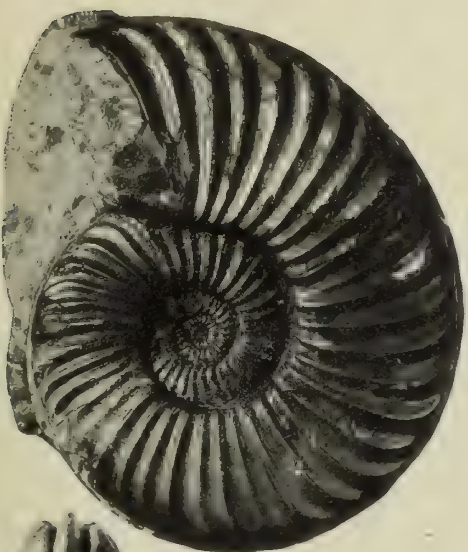
Fig. 1. *Schlotheimia extranodosa* (Waehner). Herford, Westphalia. BM. C31408. × 1.

Fig. 2. *Schlotheimia complanata* von Koenen. Osterwald, Westphalia. Holotype, figured by von Koenen, 1902 : 9, pl. 7, figs. 4–6. Geologisches Institut, Göttingen, 192. × 1.

Fig. 3. *Arietites bucklandi* (J. Sowerby). Manor Road Quarry, Keynsham, Somerset. Bristol University, Geology Dept., 208. × ½.

Fig. 4. *Coroniceras* (*Metophioceras*) *conybeari* (J. Sowerby). Near Bath, Somerset. Holotype, figured by J. Sowerby, 1816, pl. 131. BM. 43971. × ⅔.

Fig. 5. *Schlotheimia angulata* (Schlotheim). Strasdorf, Württemberg. BM. C1408. × 1.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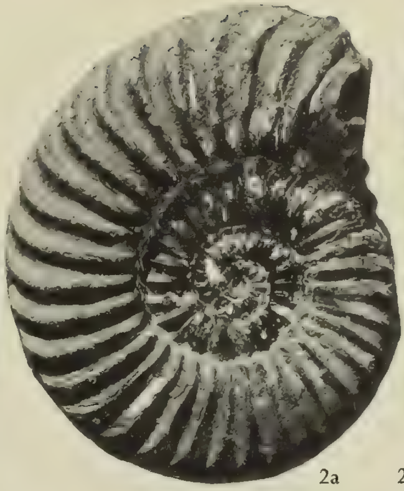
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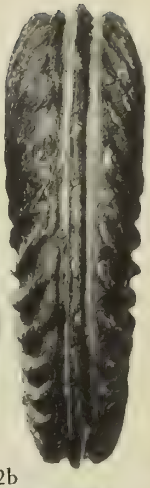
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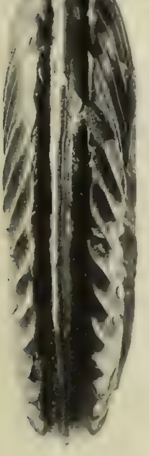
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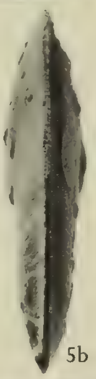
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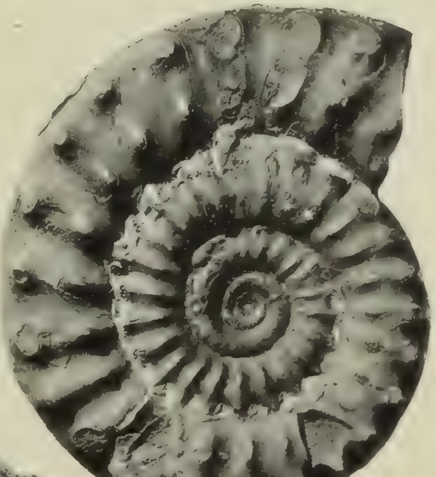
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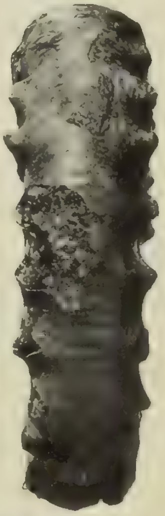
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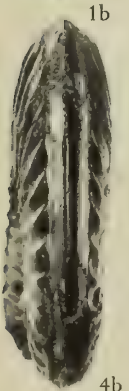
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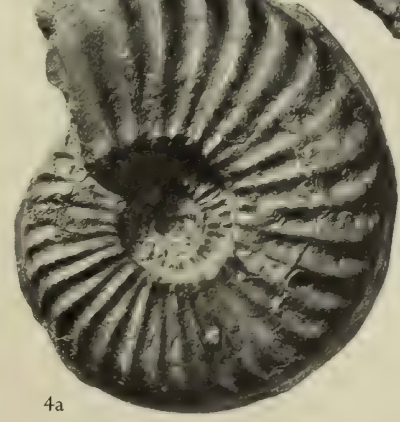
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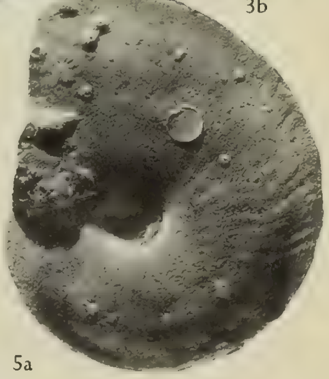
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LOWER AND UPPER SINEMURIAN ZONAL AMMONITES

PLATE 67

FIG. 1. *Asteroceras obtusum* (J. Sowerby). Charmouth, Dorset. BM. C56065. × $\frac{5}{8}$.

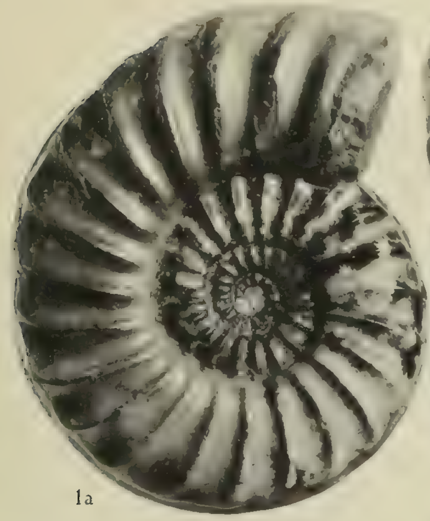
FIG. 2. *Asteroceras stellare* (J. Sowerby). Lyme Regis [Charmouth], Dorset. Lectotype, figured by J. Sowerby, 1815 : 211, pl. 93. BM. 43969*a*. × 1.

FIG. 3. *Oxynoticeras oxynotum* (Quenstedt). Cheltenham, Gloucestershire. BM. 37794. × $\frac{3}{4}$.

FIG. 4. *Oxynoticeras simpsoni* (Simpson). Robin Hood's Bay, near Whitby, Yorkshire. Figured by Tate & Blake, 1876 : 291, pl. 8, fig. 4. BM. C17903. × $\frac{3}{4}$.

FIG. 5. *Crucilobiceras densinodulum* Buckman. Charmouth, Doreset. BM. 24177. × 1.

FIG. 6. *Leptechioceras macdonnelli* (Portlock). [Larne, Co. Antrim, Ireland]. Figured by Buckman, 1923, pl. 443. BM. C41756. × 1.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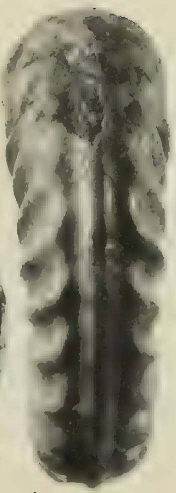
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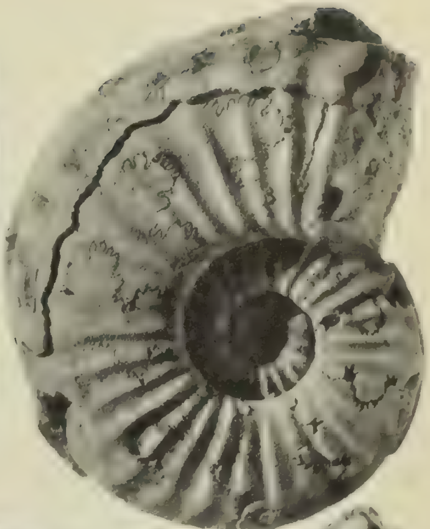
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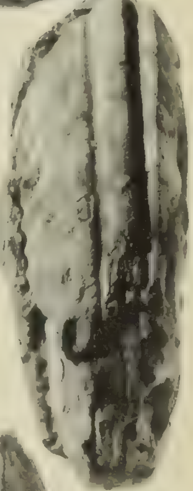
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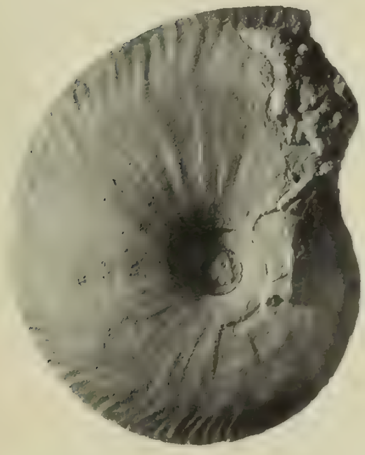
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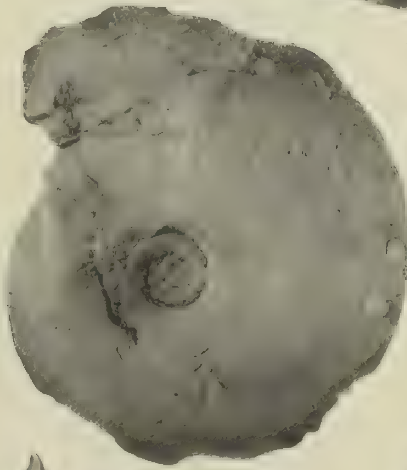
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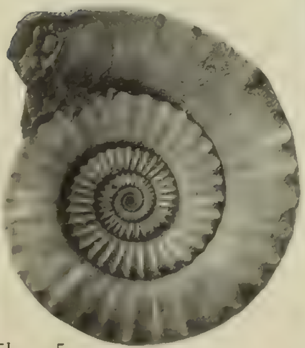
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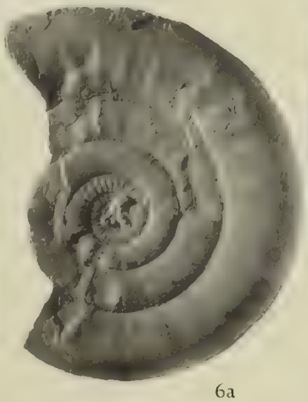
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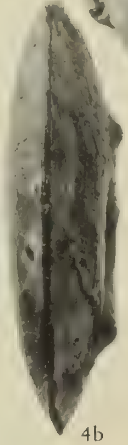
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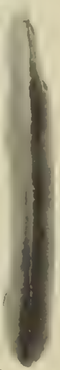
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UPPER SINEMURIAN ZONAL AMMONITES

PLATE 68

Fig. 1. *Echioceras raricostatum* (Zieten). Radstock, Somerset. BM. C56064. × ¾.

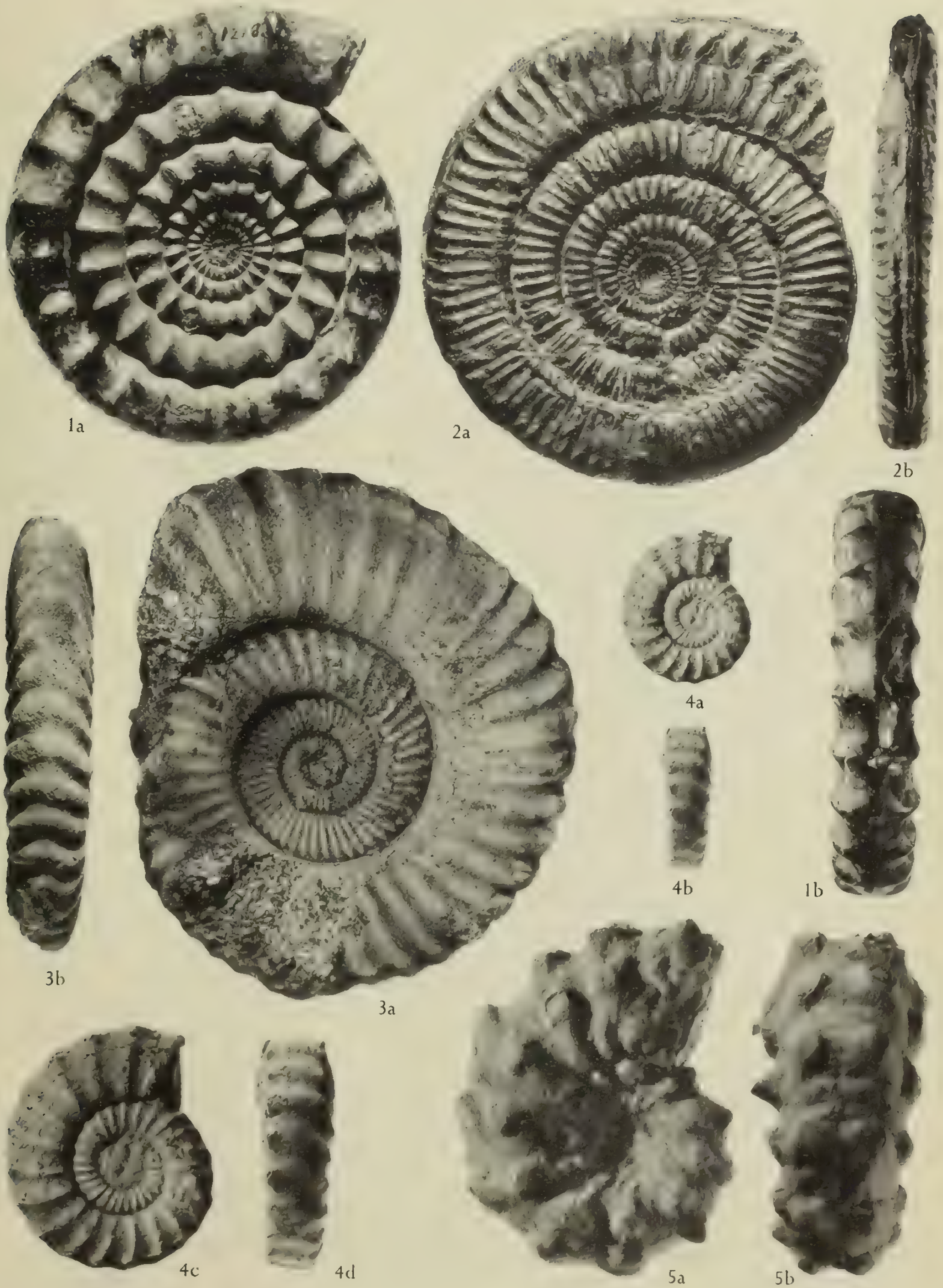
Fig. 2. *Paltechioceras aplanatum* (Hyatt). Robin Hood's Bay, near Whitby, Yorkshire. BM. 37999. × ¾.

Fig. 3. *Uptonia jamesoni* (J. de C. Sowerby). Mungar, near Radstock, Somerset. Figured by Wright, 1882 : 352, pl. 51, figs. 1, 2. BM. C2207. × ½.

Fig. 4. *Polymorphites polymorphus* (Quenstedt). Gloucestershire. BM. C50549. Figs. 4*a*, *b*, × 1 ; figs. 4*c*, *d*, × 1½.

Fig. 5. *Phricodoceras* aff. *taylori* (J. de C. Sowerby). Robin Hood's Bay, near Whitby, Yorkshire. BM. C17981. × 1. This species cannot be properly interpreted until the holotype is found or a neotype designated ; the holotype is known to have been presented to the Norwich Museum, but at present it cannot be found.

PLATE 68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1b
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4d
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UPPER SINEMURIAN AND LOWER PLIENSBACHIAN ZONAL AMMONITES

PLATE 69

Fig. 1. *Platypleuroceras brevispina* (J. de C. Sowerby). Pabba, Inner Hebrides, Scotland. Holotype, figured by J. de C. Sowerby, 1827 : 106, pl. 556, fig. 1. BM. 43915. × 1.

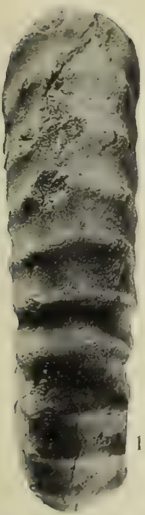
Fig. 2. *Tropidoceras masseanum* (d'Orbigny). Vallée de Saint-Pierre, near Saint-Amand, Cher. Holotype, figured in part by d'Orbigny, 1844 : 225, pl. 58. Muséum d'Histoire naturelle, Paris, coll. d'Orbigny 1643. × 1.

Fig. 3. *Androgynoceras capricornus* (Schlotheim). Amberg, Bavaria. Lectotype, described by Schlotheim, 1820 : 71. Geol.-Pal. Institut und Museum, Berlin University, Schlotheim Coll. × 1.

Fig. 4. *Tragophylloceras ibex* (Quenstedt). Watford, Northamptonshire. BM. C56638. × 1.

Fig. 5. *Acanthopleuroceras valdani* (d'Orbigny). Branch Huish, Radstock, Somerset. Figured by Neaverson, 1928 : 335. BM. C41764. × 1.

Fig. 6. *Beaniceras luridum* (Simpson). Robin Hood's Bay, near Whitby, Yorkshire. Holotype, described by Simpson, 1855 : 46 ; figured by Buckman, 1913, pl. 73. Sedgwick Museum, Cambridge, J3274. × 1.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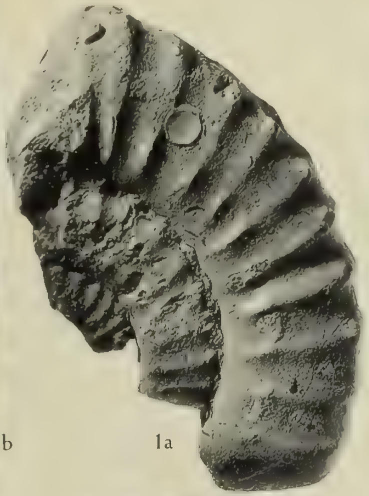
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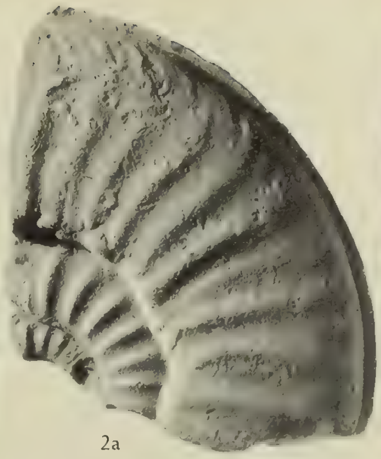
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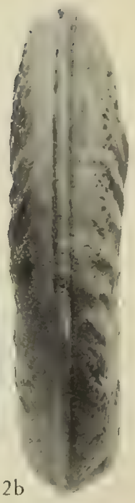
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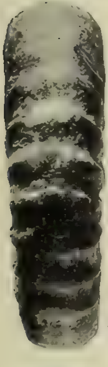
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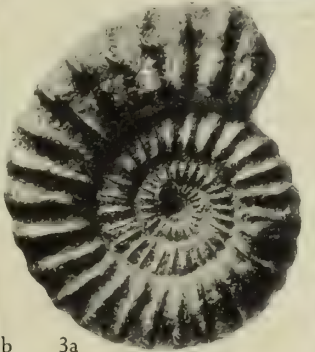
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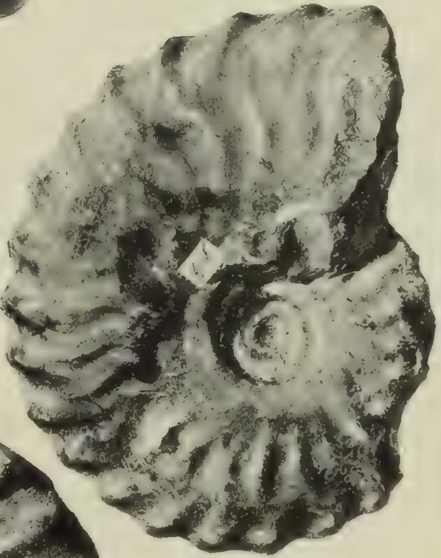
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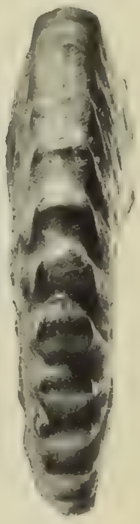
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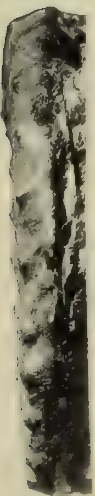
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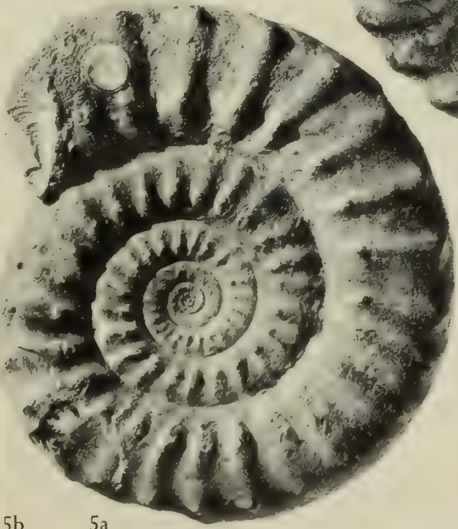
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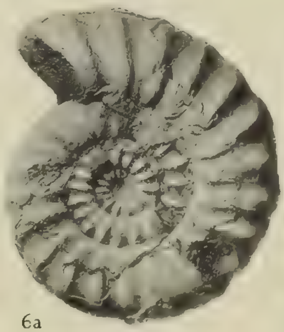
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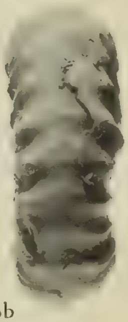
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LOWER PLIENSBACHIAN ZONAL AMMONITES

PLATE 70

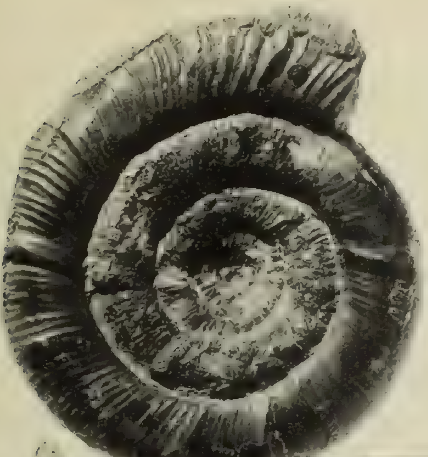
FIG. 1. *Prodactylioceras davoei* (J. Sowerby). Charmouth, Dorset. Referred to by Spath 1936 : 442. BM. 39892. × ¾.

FIG. 2. *Amaltheus stokesi* (J. Sowerby). Eype Mouth, near Bridport, Dorset. Holotype, figured by J. Sowerby, 1818 : 205, pl. 191. University Museum, Oxford, J2248. × ⅔.

FIG. 3. *Amaltheus margaritatus* de Montfort. Sandford, Dorset. BM. C6421. × ¾.

FIG. 4. *Androgynoceras maculatum* (Young & Bird). Robin Hood's Bay, near Whitby, Yorkshire. Figured by Spath, 1938 : 130, pl. 20, fig. 6. BM. C17752. × 1.

FIG. 5. *Oistoceras figulinum* (Simpson). Charmouth, Dorset. Figured by Spath, 1938 : 162, pl. 22, fig. 2. BM. 23862. × 1.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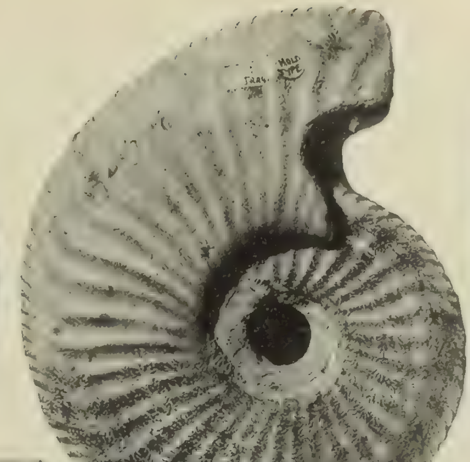
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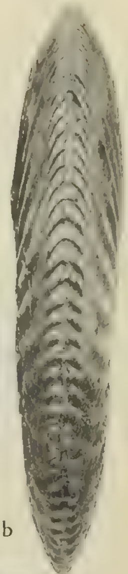
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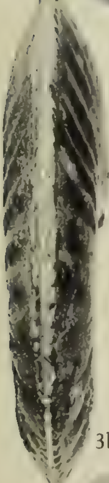
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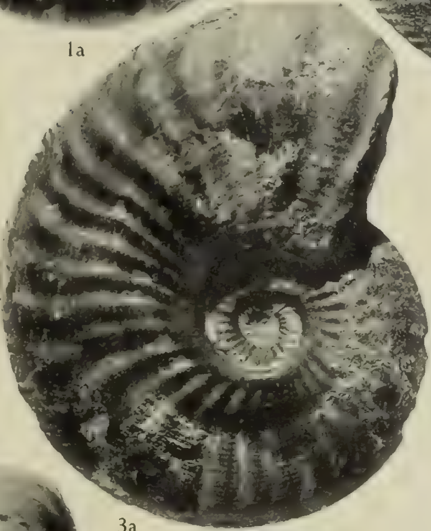
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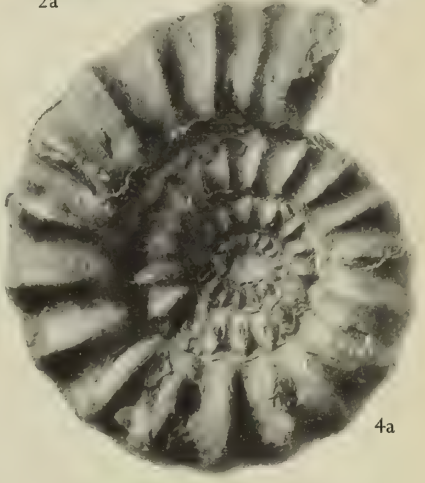
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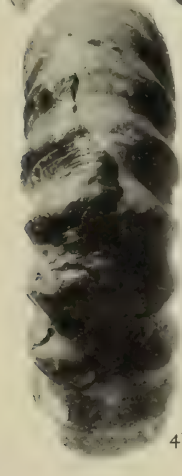
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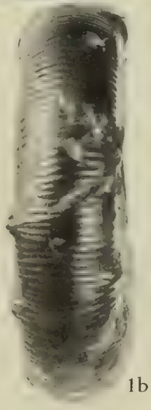
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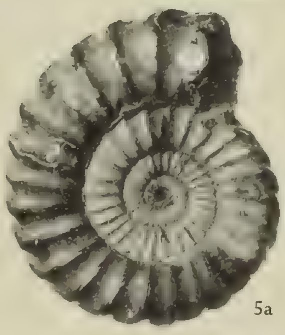
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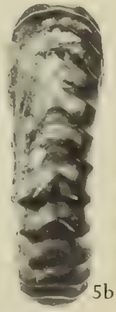
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LOWER AND UPPER PLIENSBACHIAN ZONAL AMMONITES

PLATE 71

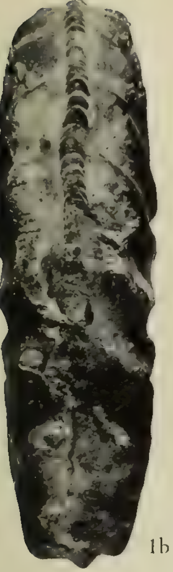
Fig. 1. *Pleuroceras spinatum* (Bruguière). South Petherton, Somerset. Neotype, figured by Howarth, 1958 : 36, pl. 7, fig. 2. Sedgwick Museum, Cambridge, J35923. × $\frac{2}{3}$.

Fig. 2. *Amaltheus gibbosus* (Schlotheim). Württemberg. BM. 50083. × 1.

Fig. 3. *Amaltheus subnodosus* (Young & Bird). Hawsker Bottoms, Robin Hood's Bay, near Whitby, Yorkshire. BM. C18073. × 1.

Fig. 4. *Pleuroceras hawskerense* (Young & Bird). Kettleness, near Whitby, Yorkshire. Figured by Howarth, 1958 : 45, pl. 9, fig. 5. Sedgwick Museum, Cambridge, J44296. × 1.

Fig. 5. *Pleuroceras apyrenum* (Buckman). Eston Ironstone Mines, Yorkshire. Holotype, figured by Tate & Blake, 1876 : 295, pl. 8, fig. 2, and by Howarth, 1958 : 35, pl. 6, fig. 1. Geological Survey & Museum, London, 24855. × 1.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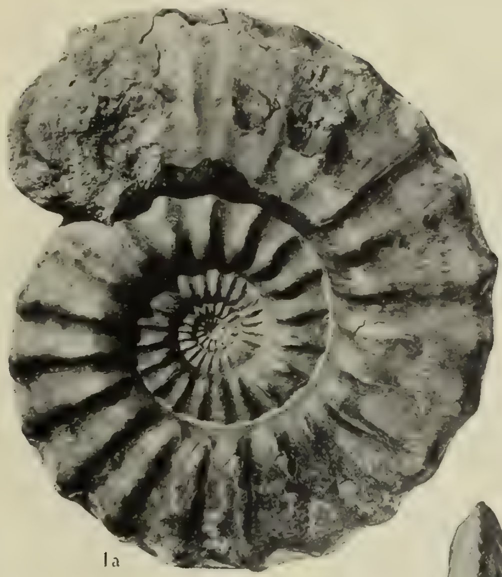
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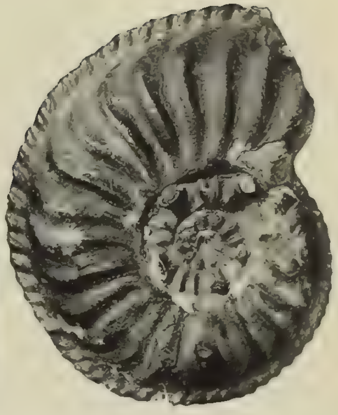
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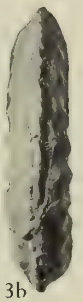
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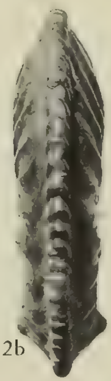
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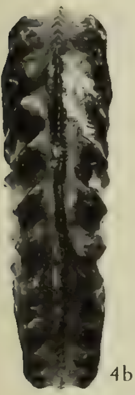
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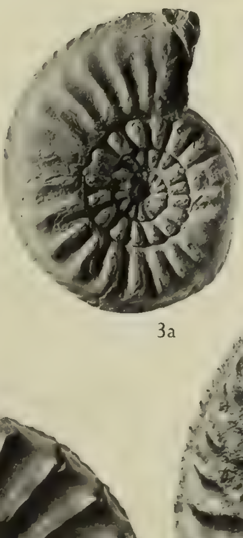
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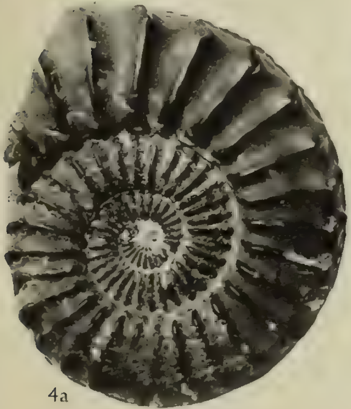
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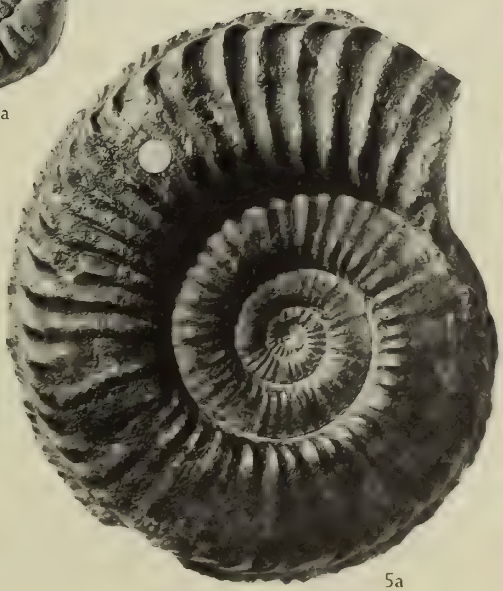
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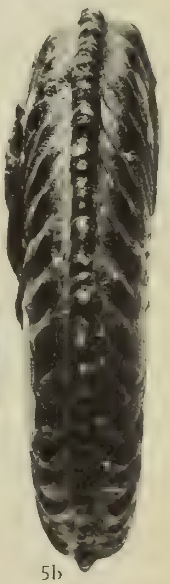
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UPPER PLIENSBACHIAN ZONAL AMMONITES

PLATE 72

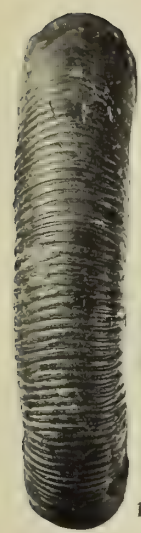
FIG. 1. *Dactylioceras tenuicostatum* (Young & Bird). Near Whitby, Yorkshire. BM. 14719. × 1.

FIG. 2. *Harpoceras exaratum* (Young & Bird). Whitby, Yorkshire. BM. C2201. × $\frac{3}{4}$.

FIG. 3. *Harpoceras falcifer* (J. Sowerby). Ilminster, Somerset. Holotype, figured by J. Sowerby, 1820 : 99, pl. 254, fig. 2. BM. 43946. × 1.

FIG. 4. *Hildoceras bifrons* (Bruguière). Whitby, Yorkshire. Figured by Buckman, 1918*a*, pl. 114. This specimen may be the holotype for it matches closely the description and figure of Lister (1678 : 205, pl. 6, fig. 2). BM. C55840. × 1.

FIG. 5. *Dactylioceras commune* (J. Sowerby). Whitby, Yorkshire. Lectotype, figured by J. Sowerby, 1815 : 10, pl. 107, fig. 2. BM. 43895*a*. × 1.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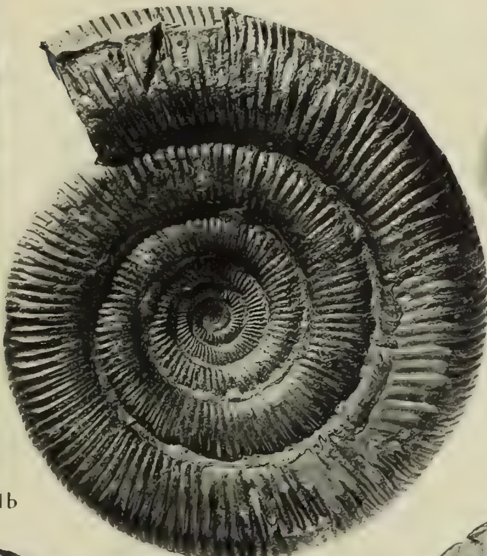
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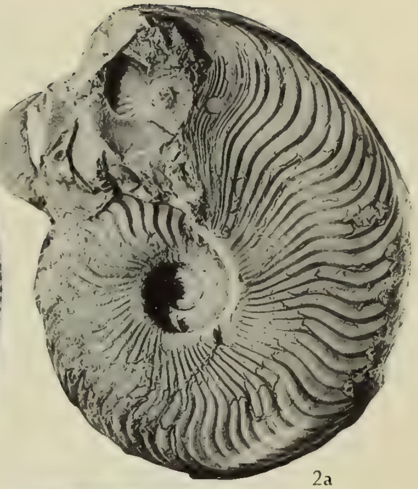
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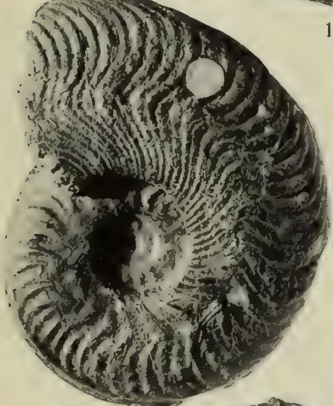
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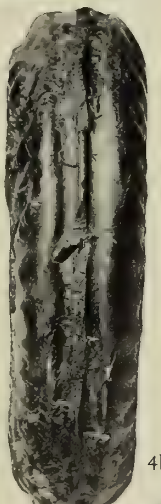
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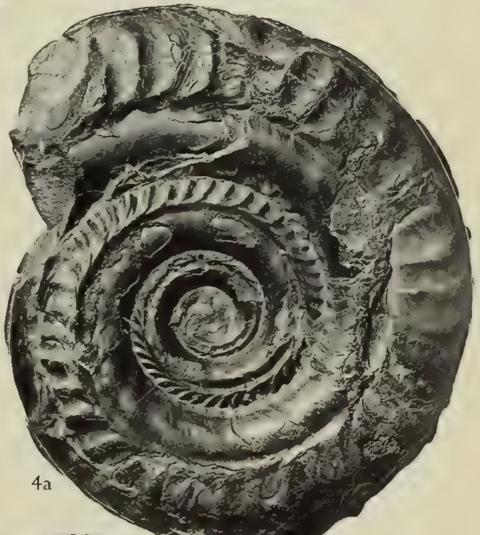
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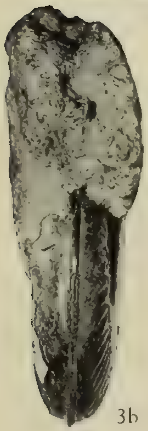
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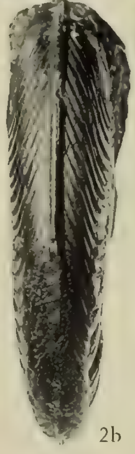
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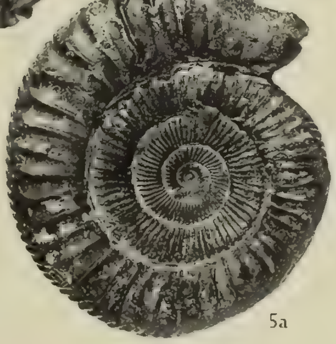
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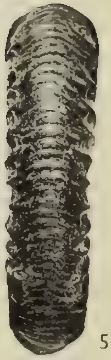
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LOWER TOARCIAN ZONAL AMMONITES

PLATE 73

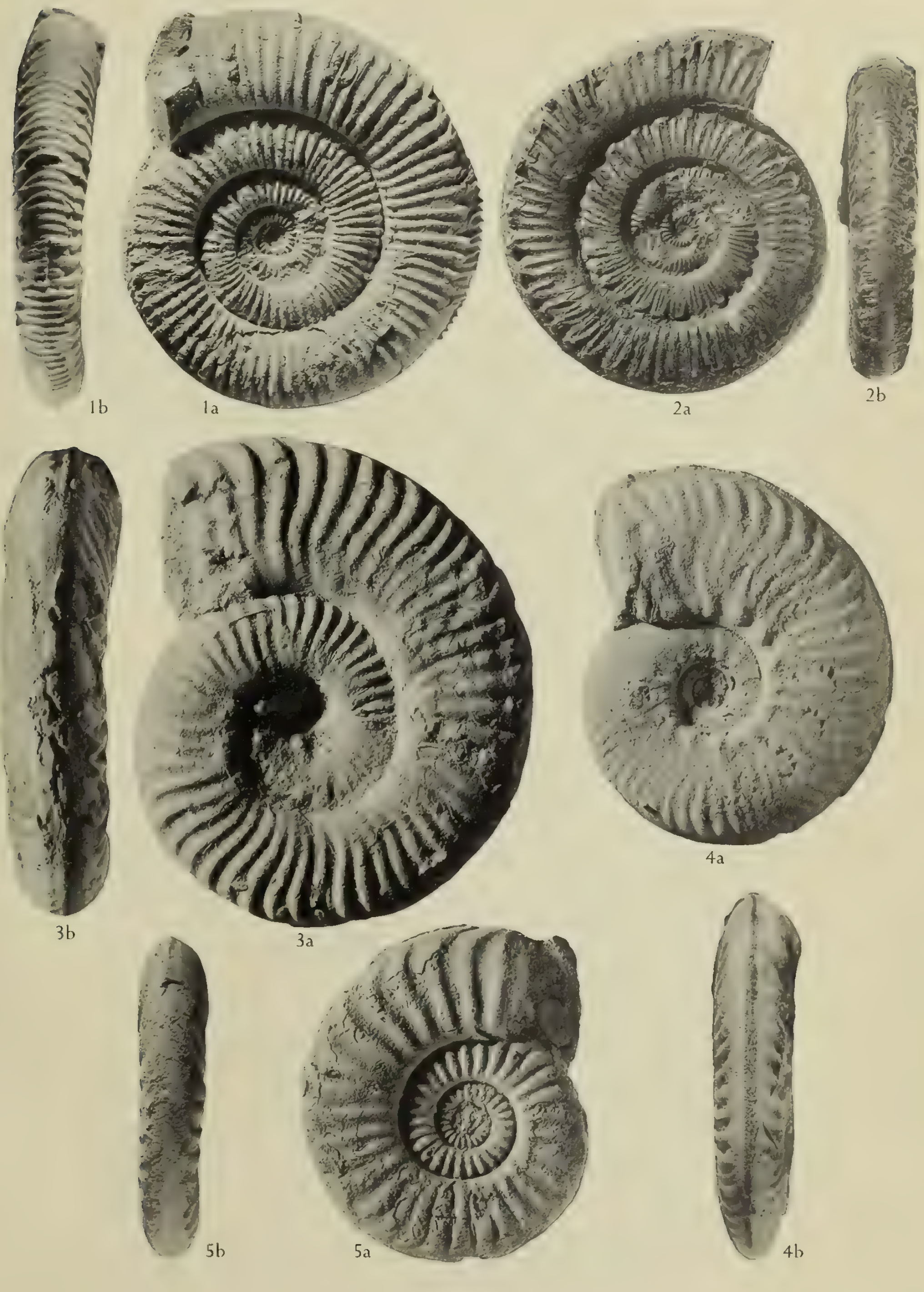
FIG. 1. *Zugodactylites braunianus* (d'Orbigny). Heyford, Northamptonshire. BM. C56067. × 1.

FIG. 2. *Peronoceras fibulatum* (J. de C. Sowerby). Whitby, Yorkshire. Holotype, figured by J. de C. Sowerby, 1823 : 147, pl. 407, fig. 2. BM. 43911. × 1.

FIG. 3. *Grammoceras thouarsense* (d'Orbigny). Thouars, Deux Sèvres. BM. C7384. × 1.

FIG. 4. *Haugia variabilis* (d'Orbigny). Amayé sur Orne, Calvados. BM. 37195. × $\frac{3}{4}$.

FIG. 5. *Dumortieria levesquei* (d'Orbigny). Wotton-under-Edge, Gloucestershire. Bristol University, Geology Dept., 11425. × 1.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5a
4b

LOWER AND UPPER TOARCIAN ZONAL AMMONITES

PLATE 74

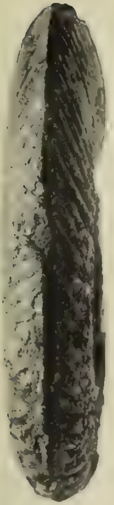
FIG. 1. *Pseudogrammoceras struckmanni* (Denckmann). Gmünd, Württemberg. BM. C1309. × ¾.

FIG. 2. *Phlyseogrammoceras dispansum* (Lycett). Frocester Hill, near Stroud, Gloucestershire. Figured by Wright, 1882, pl. 67, figs. 3, 4. BM. C1860. × ¾.

FIG. 3. *Grammoceras striatulum* (J. de C. Sowerby). Peak, Ravenscar, Yorkshire. Figured by Buckman, 1890 : 173, pl. 26, figs. 7–10. (This specimen is not the holotype which is lost.) BM. 43953. × 1.

FIG. 4. *Pleydellia aalensis* (Zieten). Hazelbury Mills, Somerset. Geological Survey & Museum, London, 69983. × 1.

FIG. 5. *Dumortieria moorei* (Lycett). Frocester Hill, near Stroud, Gloucestershire. Holotype, figured by Lycett, 1857 : 122, pl. 1, fig. 2*a*, and by Wright, 1884 : 458, pl. 80, figs. 1, 2. Geological Survey & Museum, London, 25312. × ¾.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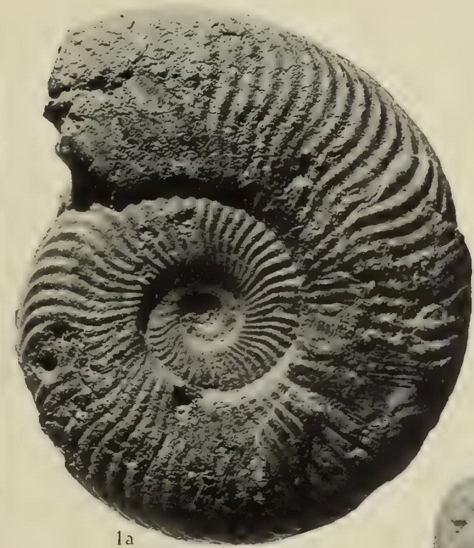
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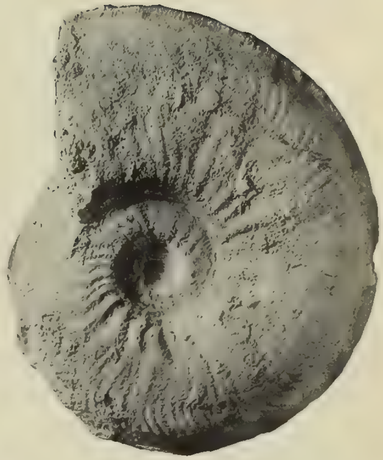
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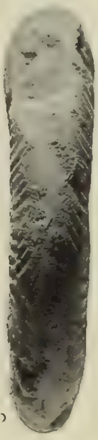
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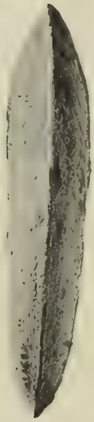
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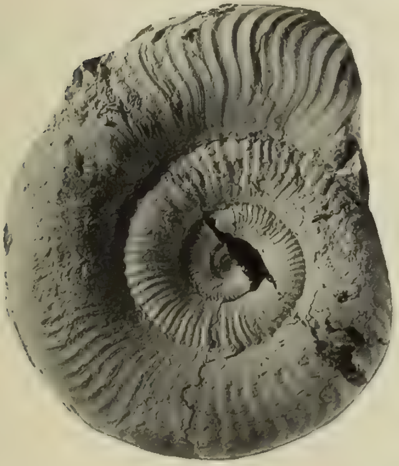
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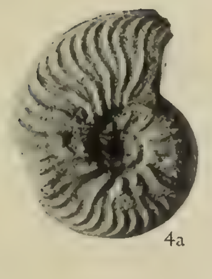
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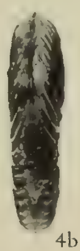
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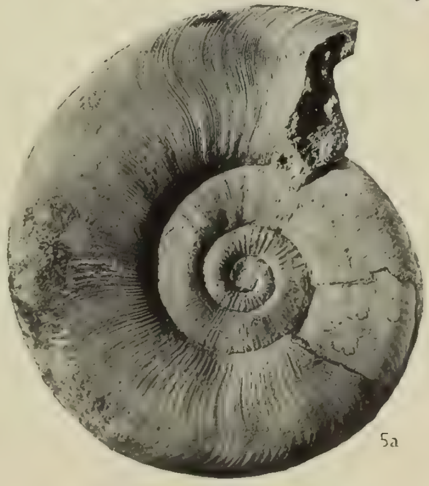
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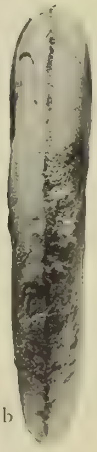
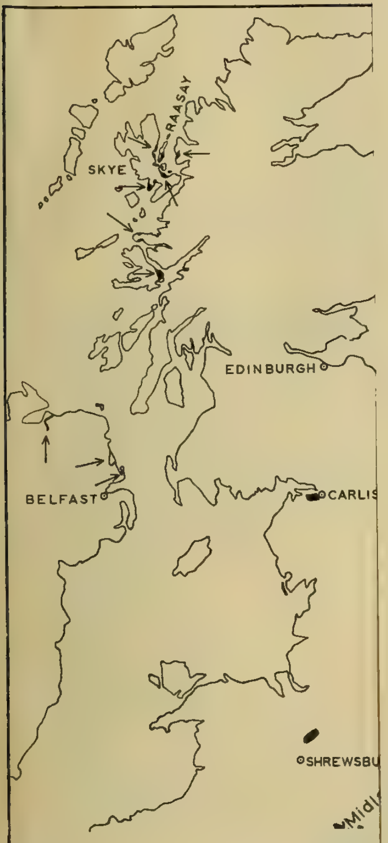

5b

UPPER TOARCIAN ZONAL AMMONITES

PLATE 75

Outcrops of the Lias in the North-west European Liassic Ammonite Province. The heavy broken line marks the southern and eastern boundary of the Province.

MUSEUM


SKYE
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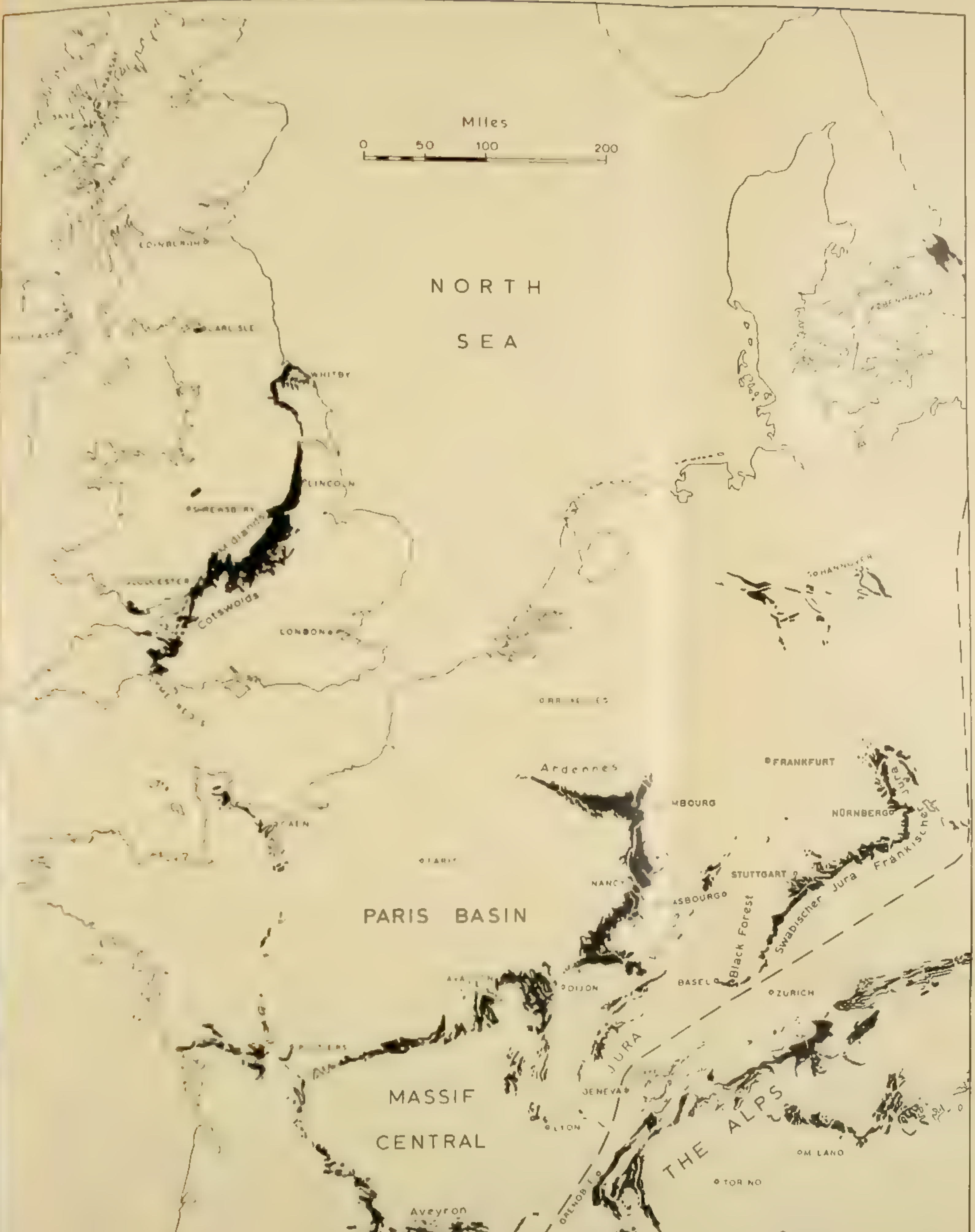
SHREWSBU
Midl


Miles
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50
100
200
NORTH SEA
EDINBURGH
CARLISLE
WHITBY
LINCOLN
SHREWSBURY
Midlands
GLOUCESTER
Cotswolds
LONDON
HANNOVER
KØBENHAVN
BRUXELLES
Ardennes
LUXEMBOURG
FRANKFURT
NÜRNBERG
Jura
Fränkische Jura
STUTTGART
Swabischer Jura
Black Forest
STRASBOURG
NANCY
PARIS
CAEN
PARIS BASIN
AVALLON
DIJON
BASEL
ZURICH
JURA
POITIERS
GENEVA
MASSIF CENTRAL
LYON
THE ALPS
MILANO
TORINO
GRENOBLE
Aveyron
AVIGNON
TOULOUSE
MARSEILLE
PYRENEES
FIRENZE

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